PATTERN EVOKED RESPONSES--
SPATIAL AND TEMPORAL FREQUENCY INTERACTIONS

BY

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Visual evoked potentials from the scalps of five human volunteers were recorded in response to 180° phase shifts of simple (single spatial frequency) and complex (sum of two spatial frequencies) sinusoidal gratings of two and six cycles/degree in a 5° field. Steady-state responses were obtained by reversing the contrast of the gratings (counterphasing) at seven shifts/second, either abruptly (square mode) or smoothly (sine mode). Each eye always received the same total amount of light during stimulus presentations, whether monocular, binocular or dichoptic. Sine mode counterphasing enhances the second temporal harmonic component of the evoked waveform, leading to a doubled response peak per stimulus shift. Square mode counterphasing generates a response with essentially all the power at the fundamental temporal

frequency. With complex gratings (2 + 6 cycles/degree), the temporal fundamental to second harmonic ratio is enhanced when the two grating spatial components are at 0^{o} relative phase angle. Gross amplitude did not differ between sine and square mode evoked responses, nor between two and six cycles/degree gratings. Hypothetical (synthetic) responses to complex gratings were computed by digitally adding the observed responses to simple gratings presented alone. These synthetic responses were significantly greater in amplitude than any observed response to the presented complex gratings, indicating that the observed response is not a linear superposition of the responses to the individual grating components. Response amplitudes ranked significantly by condition: binocular>dichoptic>monoptic, indicating that masking of one grating by another simultaneously presented in the fellow eye did not occur. Pearson correlation coefficients calculated between all possible pairs showed that, in the best possible case, only 61% of the variance of the observed dichoptic sum of gratings response can be accounted for by the contribution of the responses to the simple gratings alone. It is concluded that (a) sinusoidal counterphasing stimuli lead to two stimulus events per shift as the grating fades into and out of visibility (an observed grating onset and offset) which produces peak doubling in the response waveform, (b) spatial frequency channels that are harmonically related

in a 1:3 ratio are partially additive in the suprathreshold steady-state case, and (c) the location of this interaction is probably cortical rather than precortical as the monocularly presented complex grating response does not differ from the dichoptic response.

CHAPTER I
INTRODUCTION

Since the demise of the homunculus in the pineal body after Descartes around 1600, modeling of the function of the visual system has been based on a mechanistic analysis or decomposition of a visual scene into simpler elements. These elements have been conceived in two major groupings: "features" such as edges, colors, corners etc., and "components" in a mathematical or "Fourier" sense. The putative detectors of these elements are neurons at the various levels in the quasi-hierarchical structure of the nervous system.

Pattern analysis by apparent feature detection has been demonstrated in monkey visual cortex (Hubel and Wiesel, 1977). An order array of cortical cells seems to respond optimally to differing orientations and locations of bar or edge stimuli. A visual scene could be conceived of as an ensemble of such bars or edges. This type of analysis would, therefore, be a plausible method for mapping visual space into patterns of neural activity, especially considering the interconnectivity of those neurons (Finette, Harth and Csermely, 1978).

A visual scene can be analyzed alternatively, by analogy, along the lines of the mathematical decomposition

of a complex waveform into its components (Gaskill, 1978). This has been done optically (Switkes, Mayer and Sloan, 1978) and so raises the question of whether it is also done neurally (Kelly, 1977; Graham, 1979; Ochs, 1979).

The simplest stimulus in two dimensional visual space, in a Fourier, or spatial frequency sense, is a grating pattern whose luminosity varies sinusoidally along a single dimension (Ramirez, 1974; Kelly and Magnuski, 1975; Weisstein et al., 1977; DeValois, DeValois and Yund, 1979). In this case, there is a single component (the fundamental) at one orientation, neglecting symmetrical reflection. Gratings with different luminance profiles--square, triangular, etc.--will have multiple Fourier components. The visibility or detectability of gratings having various luminance profiles can be simply related to the strengths (power) of their spatial frequency components (Campbell and Robson, 1968). Such research, in conjunction with work using compound gratings synthesized from known spatial frequencies (Graham and Nachmias, 1971) has led to the concept of independent information "channels" in the visual system, each sensitive to a small range of spatial frequencies, and operating independently (Riggs, 1974; Quick and Reichert, 1975; Abel and Quick, 1978; Watson and Nachmias, 1980) and has led as well to clinical applications (e.g., Arden, 1979). These channels are generally conceived of as theoretical constructs, each receiving the same

inputs--the visual scene segment from the fields of its receptors--but abstracting different information to pass on to higher processors. Interactions of information within a channel can be used to model results from spatial masking experiments. An ensemble of independent channels can be used to model adaptation effects. Whether there exists a neural unit identifiable with a channel remains unclear (see Review below).

Temporal frequency channels are a logical extension of this concept; i.e., that time-varying stimuli may be detected as components (Tolhurst, Sharpe and Hart, 1973). Results from psychophysical masking experiments support a temporal sustained versus transient dichotomy, paralleling neural findings (Breitmeyer and Ganz, 1976). Such masking experiments show interactions between these presumed channels, and so have questioned the independence of Fourier channels and the Fourier model in general (e.g., Graham and Rogowitz, 1976; Legge, 1976; Bergen, Wilson and Cowan, 1979; Julesz and Caelli, 1979; Tangney, Weisstein and Berbaum, 1979). The literature review in this dissertation will examine the evidence which has been offered by both psychophysical and electrophysiological techniques. This will establish a framework for a set of experiments designed to probe spatiotemporal interactions as reflected by the pattern visual-evoked potential recorded from humans.

CHAPTER II
REVIEW OF SELECTED LITERATURE

Psychophysics

Psychophysical exploration of spatial frequency channels has developed evidence from both detection and matching paradigms. Detection experiments, such as those by Campbell and Robson (1968) and Graham and Nachmias (1971) have shown that the contrast sensitivity function defines a set of mutually independent thresholds for different spatial frequencies. By using a compound grating formed of more than one spatial frequency, a grating is detected whenever any one component exceeds its independently determined threshold. Further, gratings will be differentiated only when a component is above threshold for one grating, but not for the comparison grating (Nachmias et al., 1973; Nachmias and Weber, 1975; Isono, 1979; Ginsburg, Cannon and Nelson, 1980). Graham and Nachmias' (1971) results also show a phase independence between spatial frequencies when the components are separated by more than one octave in the high frequency ranges. These results have been extended to circular targets as well (Kelly and Magnuski, 1975).

The hypothetical structure of such channels in terms of bandwidth and sensitivity has been related to the

psychophysical thresholds for detection (Kelly, 1972; Abadi and Kulikowski, 1973; Mostafavi and Sakrison, 1976) as well as to receptive field structure (Legge, 1978b). The channels also seem to be orientation selective, as adaptation by a grating at one orientation does not raise the threshold for detection of a grating at another (Carlson, Cohen and Gorog, 1977). Such tuning, however, seems quite broad, being several minutes of arc, compared to the observed vernier accuracy of the visual system, on the order of 10 sec of arc (Blakemore and Hague, 1972; Westheimer, 1978).

Detectability or threshold level experiments, while providing much information, do not necessarily predict the behavior of the visual system in its normal, non-threshold operating ranges. Suprathreshold experiments in contrast matching and size perception have to some extent also supported the multiple parallel narrow band channels model (Watanabe et al., 1968; Frome et al., 1979; Levinson and Frome, 1979; Arend and Lange, 1980), but complications indicating some interactions between channels have been found (Stromeyer and Klein, 1975; Tangney, Weissten and Berbaum, 1979). Composite pattern adaptation effects have indicated an inhibition between channels (Stecher, Sigel and Lange, 1973). Nonindependence has also been found with masking patterns two octaves away (Henning, Hertz and Broadbent, 1975; Cavanaugh, 1978; Klein and Stromeyer, 1980), with phase perception (Stromeyer, Lange and Ganz,

1973; Atkinson and Campbell, 1974; Arend and Lange, 1979; Burr, 1980) and with sensitivity increases by certain masks (Tolhurst and Barfield, 1978).

Alternative models for pattern perception have assumed some form of broad band channel or channels in parallel or replacing the narrow band array (Stromeyer and Klein, 1974; Kulikowski and King-Smith, 1973; Kulikowski, Abadi and King-Smith, 1973; Spitzberg and Richards, 1975; Snyder and Srinivasen, 1979; Arend and Lange, 1979). Wilson and Bergen (1979) and Bergen, Wilson and Cowan (1979) reduce the number of mechanisms to four but invoke large nonlinearities to fit the data. Two-dimensional periodic patterns seem to require either size-tuned detectors or extensive interchannel interaction (Burton, 1973, 1976; Carlson, Cohen and Gorog, 1977; Tyler, 1978a). On the other hand, phase channels as well as spatial frequency channels have been proposed (Bacon, 1976). Interactions are also demonstrated with binocular stimuli (Blake and Levinson, 1977; Legge, 1979; Walker and Powell, 1979; Blake and Rush, 1980; Cormack and Blake, 1980) and dichoptic masking experiments (Abadi, 1976).

Cortical location of these channel interactions, and specifically inhibition of neighboring columns as postulated by Abadi (1976), while often assumed, need not be the only determinant of spatial frequency selectivity, although there seems to be a progressive tuning to sharper selectivity by each stage in the visual pathway

(Armington, Gaarder and Schick, 1967; Armington, Corwin and Marsetta, 1971; Maffei and Fiorentini, 1973; Armington, 1977). Kelly (1975), by postulating receptive field coherence, has presented a retinal model. Retinal field size for channels has been described by Quick and Reichert (1975) who maintained that the channels had a constant retinal area independent of center frequency. This is flatly contradicted by Hoekstra et al. (1974) and by Howell and Hess (1978), who found a critical response amplitude dependence on the number of cycles present in the display to avoid artifactual decreases in recorded sensitivity, and also in part by a series of papers by Koenderink et al. (1978) in which target extent in the visual field had a critical effect on detection. Kelly's (1976) specific attempt to infer a postretinal location for Fourier channels showed that for the mechanisms he tested, the achromatic and opponent-color pathways were equally affected by pattern adaptation, and so presumably the effects occurred prior to a neural locus at which these two pathways specialize, although color discrimination by spatial frequency channels remains in debate (Ingling, 1978; King-Smith and Carden, 1978). Orientation effects are usually assumed to require cortical processing, however, since it is in the cortical cells that orientation selectivity of neural elements seems most strongly expressed, as determined by cat and monkey studies (Bisti and Maffei, 1974; Boltz, Harwerth

and Smith, 1979; Bauer et al., 1979; Berkeley, Kitterle and Watkins, 1975; Hubel and Wiesel, 1977; among others), and also apparent from studies with pattern evoked retinal responses (Maffei and Campbell, 1970).

Modulating the stimuli in the temporal domain by flickering or counterphasing the grating leads to changes in contrast sensitivity (Kelly, 1977; Koenderink and van Doorn, 1979. Such temporal stimuli can also be examined from a Fourier analysis viewpoint. The interdependence of temporal and spatial channels can be seen in the effect of temporal modulation of a grating on the "oblique effect," a decrease of response or of sensitivity to stimuli in non-horizontal or -vertical presentations (May et al., 1979); the effect is apparent only at low temporal frequencies (Camisa, Blake and Lema, 1977). Selectively masking "sustained" channels appears to uncover several "transient" channels with differing peak sensitivities (Legge, 1978a). Kelly (1979a) using stabilized-image stimuli has shown, that without some temporal modulation such as that provided by the slow drift of a "fixated" eye, thresholds are elevated by a factor of 20. Using inverse Fourier transforms, Kelly constructed line spread functions from the stabilized velocity data that closely resemble those derived by localized but unstabilized stimuli and with electrophysiologically determined receptive field structures (Braddick, Campbell and Atkinson, 1978; Legge, 1978b; Kelly, 1979b).

Electrophysiology

With the advent of signal averaging computers, electrophysiological data from humans could be taken with high enough signal-to-noise ratios to be generally useful, both as a research tool (Riggs and Wooten, 1972; MacKay and Jeffreys, 1973; Riggs, 1974, 1977), and as a clinical diagnostic technique (Sokol, 1976; Sherman, 1979). Such data, generally stimulus-evoked potentials, occupy an intermediate area in stimulus-response analysis, between cellular or unit recording in neural networks, as in retina (Dowling, 1970) or cortex (Hubel and Wiesel, 1977), and whole organism responses, generally explored psychophysically. Evoked potentials sum the responses of a population of cells within the electrical range of the recording electrode, integrating them according to their strength and distance (Verzeano et al., 1968; Creutzfeld et al., 1969; Lesevre and Joseph, 1979; Legatt, Arezzo and Vaughan, Jr., 1980). Sharp depolarizations correlate well with surface positivity (Creutzfeld and Kuhnt, 1973) and reflect processes that can be isolated psychophysically (e.g., cone mechanisms: Gouras and Padmos, 1974; masking: Samoilovich and Trush, 1979) or electrophysiologically (e.g., internal/conditioned inhibition: Shul'gina, 1979; DeToledo-Morrell, Hoeppner and Morrell, 1979; pattern selective adaptation: Movshon and Lennie, 1979).

Evoked potentials, by their definition, are locked to a stimulus event, rather than a stimulus condition, although various conditions [not only experimental (Uren, Stewart and Crosby, 1979)] can have profound effects on such potentials, as a vast clinical literature atests (e.g., Ashworth, Maloney and Townsend, 1978; Ikeda, Tremain and Sanders, 1978; Kadobayashi et al., 1978; Noebels, Roth and Kopell, 1978; Rover et al., 1978; Von Knorring, 1978; Andreassi et al, 1979; Arseni et al., 1979; Facciolla et al., 1979; Frank and Torres, 1979; Kataoka et al., 1979; Klassen et al., 1979; Naparstek et al., 1979; Seppalainen, Raitta and Huuskonen, 1979; Shagrass et al., 1979; Sokol and Nadler, 1979; Wolfe, 1979; Wright, Craggs and Sergejew, 1979; Lee et al., 1980; Regan et al., 1980; among others). Visual acuity testing has used the evoked potential in addition to psychophysical tests to assess objectively spatial frequency characteristics of the visual system and to prescribe corrective refractions (Sokol, 1972; Arden and Lewis, 1973; Bodis-Wollner and Diamond, 1976; Bostrom, Keller and Marg, 1978; Hess, Howell and Kitchin, 1978; Hofmann, Bartl and Gruber, 1978; Enoch, Bedell and Kaufman, 1979; Enoch, Campos, Greer and Trobe, 1979; Enoch, Ohzu and Itoi, 1979; Enoch, Yamade and Namba, 1979; Klingaman and Moskowitz-Cook, 1979; Tyler et al., 1979; Dobson and Davison, 1980; Julesz, Kropfl and Petrig, 1980; King-Smith and Kulikowski, 1980).

Evoked potential research to demonstrate spatial frequency channels has used both masking and adaptation paradigms, as in similar psychophysical work (Ochs and Aminoff, 1980). The classic experiment by Campbell and Maffei (1970) used a grating of a specified spatial frequency to adapt a channel, and by sampling spatial frequencies near it with counterphasing gratings, Campbell and Maffei demonstrated a selective suppression of the evoked response until the test grating was at least an octave away from the adapting grating. Similarly, rotation of a test grating at the same spatial frequency as the adapting grating showed a 15^{o} specificity for orientation of a particular channel, paralleling psychophysical results. Some differences from psychophysical data have also been demonstrated; recovery of the depressed evoked potential response is much faster than the recovery of the contrast detection threshold (Mecacci and Spinelli, 1976). Other work, however, shows close correspondences with psychophysics (e.g., contrast thresholds: Adachi-Usami, 1979; Kojima and Zrenner, 1980). Direct comparison of electrophysiologic and psychophysiologic measures of apparent contrast shows close correlations with each other and indicates that the evoked potential can be an accurate reflection of perceptual experience (Bodis-Wollner, Hendley and Kulikowski, 1972; Franzen and Berkeley, 1975).

Temporal frequency channels, usually conceived as a dichotomous set of parallel transient and sustained mechanisms, have been implied by evoked responses to both slow reversal rate stimuli and by temporal tuning curves using higher rates of stimulus presentation (Lennie, 1980). Such stimuli are sorted in evoked potential research into two broad overlapping classes according to stimulation rate: "steady-state" and "transient" response recording. Steady-state recording presupposes a temporally periodic stimulus presented for a sufficiently long period of time that the effects of the abrupt onset of stimulation are no longer apparent (Regan, 1977). Transient evoked potentials, by contrast, deliver one stimulus and wait until the response to that stimulus has returned to background activity before presenting the next (Kinney, 1977). In nonlinear signal processing systems, the steady-state response is not necessarily equivalent to the superposition of the transient responses at the same rate. In this regard, the evoked potentials do not behave as a linear system. Patterns of signal buildup and decay with various time courses and differing arousal states have demonstrated this essential nonlinearity in cortex (Steinberg, 1965; van der Tweel and Verduyn Lunel, 1965).

The analysis of steady-state activity also gives information on the visual pathways in the form of phase lag and permits the modeling of the signal processing system as a resistor-capacitor (R-C) network or frequency

filter (Bode, 1945). Amplitude (or power) alone can only provide information on the resistive elements of a system; phase information is required in addition to permit a full description of a system's behavior. Additionally, steady-state recording permits the separation of low versus high temporal frequency "channels," i.e., the modeling of the visual "processor" as a temporal Fourier analyzer (Jones and Keck, 1978; Graham, 1979). Such separation shows a strong interaction with spatial frequency. By using transient stimuli, Jones and Keck (1978) were able to show that there were at least two mechanisms responding to the stimuli. One had a short latency component and was strongest at 1 or 2 cycles/degree, saturated at low contrast, and appeared insensitive to precise retinal location. The major component was tuned to higher spatial frequencies and showed a linear response with log contrast. This type of response was also found by Regan (1978) using an online analog Fourier analyzer and steady-state recording. Responses to low spatial frequencies seemed enhanced with fast stimulus presentation rates, and high spatial frequencies with low reversal rates. These data support a model of the visual system with many parallel channels that are specific to spatial frequency, temporal frequency and orientation, all with relatively narrow bandwidths, and permit the description of the system response in terms of a spatiotemporal response surface defined on purely

electrophysiological criteria (Tyler, Apkarian and Nakayama, 1978). This surface has been shown to be homologous to the data derived from psychophysical contrast detection threshold studies (Barris and Dawson, 1980). Relative spatial phase detection, however, seems to require either channel interaction, separate broadly tuned channels, or an additional class of mechanisms specifically sensitive to phase (e.g., Burr, 1980; Ross and Johnstone, 1980).

Analysis of cat and monkey cortical neurons has revealed a possible cellular basis for the Fourier model of visual processing (Maffei and Fiorentini, 1973). Hubel and Wiesel's (1977) model of monkey cortex as an ensemble of bar detectors has been recast as an ensemble of spatial frequency detectors (Noda et al., 1971; Maffei, 1978; Movshon, Thompson and Tolhurst, 1978a, 1978b, 1978c; Kulikowski, 1979). This model seems to fit the tuning curves for the neurons better as the cells show a greater selectivity when tested by gratings rather than bars (Albrecht, DeValois and Thorell, 1979), although the concept has been extensively debated (see for example Glezer, Ivanoff and Tscherbach, 1973; Tyler, 1975; Glezer, 1975; Glezer et al., 1976; Tyler, 1978b; Glezer, 1979). DeValois, DeValois and Yund (1979) directly tested the concept of "Fourier" tuning in cortical neurons and found that both simple and complex cells were sensitive to the orientation of the optical Fourier transform components of

a pattern, rather than the orientation of the edges. This sensitivity applied also to the spatial frequency axis, as the response to the higher harmonics of square edged and missing fundamental patterns was predicted by the Fourier components (Maffei et al., 1979a). At lower spatial frequencies, however, some edge detection does occur (Maffei et al., 1979b; Kulikowski and Bishop, 1980; Ross and Johnstone, 1980).

Binocular Data

The existence of two functional "simultaneously" seeing eyes in the normal human, and the assumption of singular independent information channels immediately raises the problem of binocular integration. Do the two eyes constitute separate visual channels (Cormack and Blake, 1980)? By using the performance degrading effects of stimulus uncertainty on grating detection, Cormack and Blake (1980) were able to show that eye-of-origin uncertainty was unable to degrade detection in stereo-normal subjects, but did lower performance in stereo-blind subjects, thus indicating that the two eyes, at threshold, normally behave as a single channel. However, especially at suprathreshold levels, the separateness of information from the two eyes is not lost at higher levels. Binocular rivalry, or alternating monocular suppression during dichoptic viewing, compounds the problem of spatial frequency channels and perceptual

fusion (Julesz, 1978). However, even in nondichoptic situations, i.e., with perceptual fusion, Makous and Sanders (1978) were able to show that some monocular suppression remained.

The neural location of this suppression remains unclear as neither evoked potentials need be reduced, nor McCollough color aftereffects weakened, by a perceptual invisibility of the inducing stimuli (Cobb, Morton and Ettlinger, 1967; White et al., 1978). Binocular suppression, or facilitation, when measured by evoked potentials, seems critically dependent on the stimulus parameters, and has generated apparently contradictory results. If the images from the two eyes are not perceptually fused, suppression results; if the images are disparate, but do fuse, enhancement results; if only a blank field is presented to one eye, that eye is apparently ignored (Ciganek, 1971; Harter, 1977). Individual components of the transient evoked potential behave differently with differing spatial frequencies and orientations (Harter, Seiple and Salmon, 1973; Harter, Seiple and Musso, 1974; Harter, Condor and Towle, 1980). Active suppression of an artificially blurred image in one eye has been demonstrated with steady-state evoked potentials (Fiorentini et al., 1978) and has been correlated with similar results found in human amblyopia (Srebro, 1978; Wanger and Nilsson, 1978; Levi, Harwerth and Smith, 1979). Temporally disjoint but spatially

identical and fused stimuli produce a reduction of steady-state evoked potentials in stereo-normals but a smaller reduction in humans with impaired binocular vision (Lennerstrand, 1978a). Inducing greater binocular rivalry by changing the color and pattern presented to each eye resulted in a perceptual suppression/alternation, but the evoked response did not reflect the rivalry (Lennerstrand, 1978b). In fact, the signal depression was greater with no spatial disparity, supporting the hypothesis that the depression due to the temporally disjunct stimulation was producing interference in a single spatial frequency channel, as a form of stimulus masking. Unit analysis has shown neurons "tuned" for interocular disparity (Fischer and Kruger, 1979; Poggio, 1979) but the variability of the response is so great that a "variability" code has been proposed (Crawford and Cool, 1970) since occlusions of response as well as facilitation have been found (Noda, Creutzfeld and Freeman, 1971). Binocular response of striate cells seems dependent on the corpus callosum (Payne et al., 1980) and would imply a separable evoked response for each eye. In sum, these data would seem to indicate that at least some aspects of depressed detection reside in the neural elements of the primary visual cortex, even if perceptual rivalry may not (Martin, 1970).

Summary

To recapitulate the main findings detailed above: (a) psychophysical data from detection, discrimination and masking experiments have been modelled as spatial and/or temporal frequency channels, responsive to Fourier components of stimuli; (b) electrophysiological recordings at the single unit level in area 17 are consistent with activation by spatio-temporal Fourier components; (c) stimulus evoked potentials, although recording neural discharges *en masse*, can be manipulated meaningfully by appropriate changes in stimulus Fourier components; and (d) data from psychophysical, evoked potential and single-unit recording experiments suggest that eye-of-origin might be an additional characteristic of the spatiotemporal frequency channels.

CHAPTER III
EXPERIMENTAL RATIONALE

The multiple channel model of visual spatial frequency analysis (Campbell and Robson, 1968) predicts independence between channels more than an octave apart. If this independence holds in the visual cortex, the response to the complex gratings will be a linear superposition of the response to the grating's components presented separately. Any interaction, constructive or destructive, will be apparent from the evoked waveform (by correlation analysis) as well as by amplitude and/or phase changes. Phase independence of sum of sinusoid gratings, predicted by the same detection experiments, will also be tested.

If the spatial frequency channels are fully independent at area 17, i.e., independent cortical columns (Hubel and Wiesel, 1972), then the mode of stimulus component addition should not change the response, i.e., haploscopic (dichoptic) presentation of a complex grating should equal monocular presentation. If there is interaction, then these two modes of stimulation will indicate whether the interaction is cortical or precortical (if the response to the complex monocular

stimulus is less than that for the dichoptic input assuming destructive masking).

Lastly, by adding harmonics to a steady-state temporal stimulus (sinusoidal counterphase vs. square wave at seven shifts/second), this experiment will show whether temporal frequency channels also interact to change any of the above results. If there is no difference, the visual system is using only the fundamental stimulus frequency. If enhancement or interference occurs, the model of the visual system as a strict Fourier analyzer in the temporal domain cannot be maintained.

In conclusion, these experiments will test the degree of independence of spatial and temporal frequency channels in steady-state suprathreshold response of the human visual system. Should interaction between the channels be found, these experiments should also indicate a possible site for them (retina/LGN or primary cortex) i.e., does the eye-of-origin constitute an appropriate characteristic of a spatial frequency channel. The results link the threshold detection experiments in psychophysical research and suprathreshold visual evoked responses.

CHAPTER IV
METHODS

Subjects

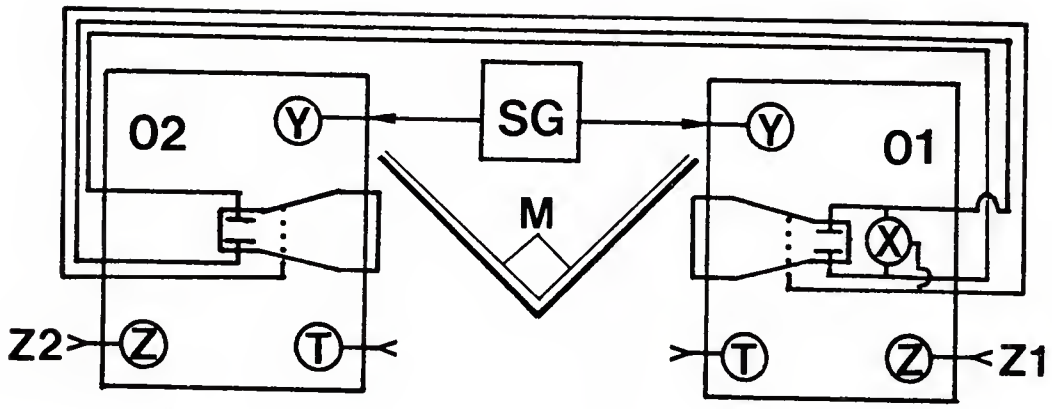
Three male and two female volunteers, Caucasian, between 22 and 30 years old, who gave their informed consent, served as subjects. The females were between menses and ovulation in their menstrual cycles. All subjects had corrected 20/20 Snellen acuities in each eye, perfect Farnsworth D-15 color discrimination tests in each eye, Titmus stereoacuity of 50 sec of arc or better, and normal binocular fusion ranges as tested by prismatic displacement of a 5^{o} target with a phoropter. Monocular contrast sensitivity curves were obtained for each eye by inspection of photographs of Arden type sine wave grating plates (Arden, 1979) and were normal in shape and approximately equal between the two eyes for each subject. All subjects practiced viewing the stimulus display before recording sessions were started. No difficulty was reported in aligning the haploscopically presented display. Subjects wore their normal corrections, and no artificial pupils were used. All subjects were tested three times on separate days, producing 15 subject-sessions of 20 stimuli each (see below).

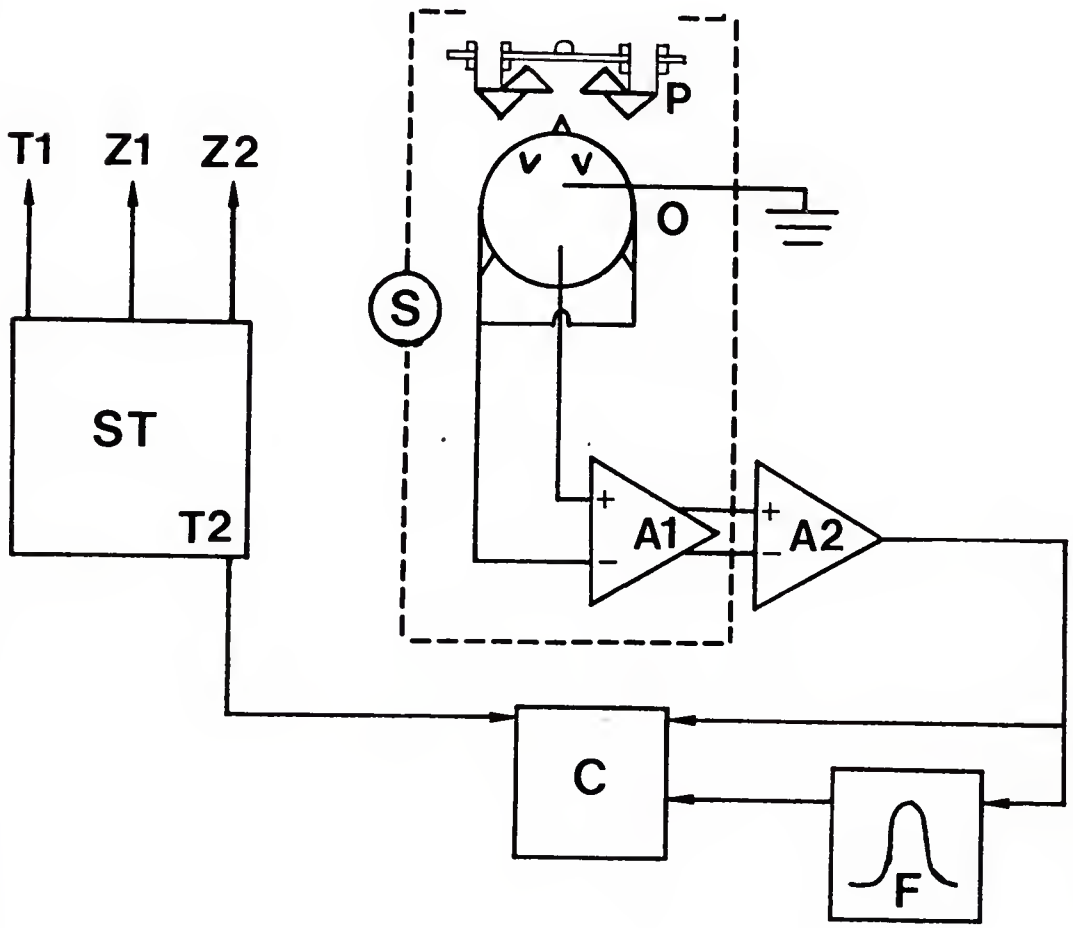
Stimulus

Two Tektronics RM503 oscilloscopes with blue-green (P2) phosphors were mounted to face each other (Fig. 1). Two first surface mirrors were mounted between them to direct the respective images to a set of prisms mounted on rotating sleeves, permitting adjustment for individual interpupillary distances. The circular oscilloscope screens subtended 5^{o} of arc at the eye. Fixation and fusion were aided by providing a black fixation spot of 22'48" in the center of each screen (two subjects) or diagonal crosshairs of 00 black silk of 1'53" diameter (three subjects). No significant differences were noted in control runs with one subject in response wave form, amplitude or phase with the different fixation marks in distinction to some psychophysical results (Weisstein, et al. 1977). The horizontal deflection plates of CRO#2 (slave) were connected in parallel to those of CRO#1 (master) to insure perfect synchrony of sweep, triggering and unblanking as well as phase lock between the two displays.

Vertical sine wave gratings were generated on the oscilloscope faces by modulating the z (luminance) axes with the appropriate waveform (Campbell and Robson, 1968). A mean luminance field was established with a 0.55 MHz signal from an external function generator fed to the x-inputs of the oscilloscopes. The field was refreshed at 1.56 KHz and provided approximately 140 traces per degree

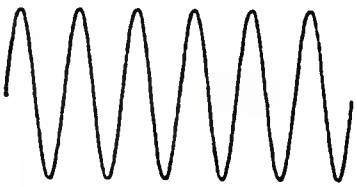
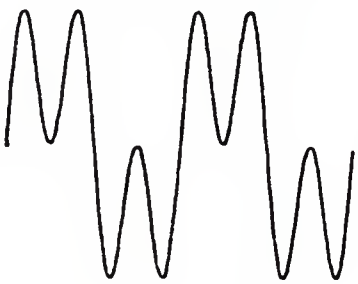
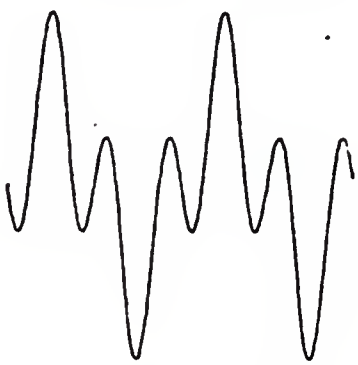
Figure 1. Schematic illustration of stimulus and recording arrangement. A1, A2: preamplifiers; C: computer; F: band-pass filter; M: first-surface mirrors; O: observer; O1: master display oscillosocpe; O2: slave display oscilloscope; P: prism array; S: shield room; SG: signal generator; ST: stimulus control circuitry; T: oscilloscope trigger input; T1: ocilloscope trigger signals; T2: computer trigger signal; X: master oscilloscope horizontal control; Y: oscilloscope vertical control; Z: oscilloscope luminance control input; Z1, Z2: luminance control signals to O1 and O2 respectively.


02
Y
SG
Y
01
M
X
Z2
Z
T
T
Z
Z1


T1
Z1
Z2
P
v
v
O
S
ST
T2
A1
A2
C
F

of visual angle. Due to the line spread of the phosphor, the individual traces were completely unresolvable. The brightness was adjusted to 5.16 cd/m^2 at the eye although this level is not critical for contrast evoked potentials (van der Tweel, Estevez and Cavonius, 1979). The AC signal from the stimulus circuitry (see Appendix) modulated the luminance of the screens around this value. The high refresh rate and the stable triggering of the oscilloscopes prevented variability of the counterphasing stimulus, such as found in television systems (van Lith, van Marle and van Dok-Mak, 1978; Meienberg et al., 1979). Luminance profiles of four shapes were used (Fig. 2): (1) a fundamental sine wave, (2) its third harmonic, (3) the sum of 1 and 2 at a phase angle of 0° (peaks subtract), and (4) the sum of 1 and 2 at a phase angle of 180° (peaks add) (Atkinson and Campbell, 1974). A linearity check of the screens with a photoresistor showed a distortion of 0.58% (power of the fundamental to the first harmonic) of voltage versus luminance with a 32 V sine wave grating. All stimulus waveform luminances were calibrated with a Pritchard photometer at the plane of the subject's eye and confirmed the display contrast linearity. A linear regression calculated between peak to peak voltage of the stimulus waveforms and per cent contrast ($L_{max}-L_{min}/2L_{mean}X100\%$) yielded a correlation coefficient for the line of 0.9985.

Figure 2. Stimulus luminance profile metrics for gratings used.

STIM	PROFILE	VOLTS (PP)	CD/M^2 (MAX/MIN)	CONTRAST ($\frac{MAX-MIN}{2 \times MEAN} \times 100\%$)
F 1		18	6.22/2.70	34
F 3		18	6.22/2.70	34
S 0		26	7.20/2.51	45
S 1		32	8.03/2.33	55
D C		0	5.16/5.16	0

The fundamental spatial frequency was set at two cycles per degree, producing 10 iterations of the waveform on the screen (Hoekstra et al, 1974; Howell and Hess, 1978; McCann, Savoy and Hall, 1978). The stimulus circuitry permits these waveforms to be presented monocularly (mean luminance field to the fellow eye), binocularly, and dichoptically (F1 to one eye, F3 to the other, either at 0^{O} or 180^{O} phase angle). Finally, the circuit permits the waveforms to be counterphased in two modes: sinusoidal (continuous) and square-wave (abrupt). The fundamental temporal stimulus frequency was set at seven shifts (contrast reversals) per second and modulated both the simple and complex grating phase transitions at the same rate, as suggested by Pantle (1973). These spatial and temporal frequency values are near the human contrast sensitivity peak both psychophysically (Kelly, 1977) and electrophysiologically (Bodis-Wollner, Hendley and Kulikowski, 1972; Regan, 1978). All 20 stimuli (10 sine mode and 10 square mode) were presented in each session but in different random orders and to different eyes. The stimuli were:

F1M, 2 cycles/degree, monocular presentation
F1B, 2 cycles/degree, binocular presentation
F3M, 6 cycles/degree, monocular presentation
F3B, 6 cycles/degree, binocular presentation
S0M, 2+6 cycles/degree at 0^{O} relative phase angle, monocular presentation
S0B, the same as S0M but binocular presentation
S0D, 2 cycles/degree presented to one eye, 6 cycles/degree presented to the fellow eye, the fused gratings at 0^{O} relative phase angle (dichoptic)

S1M, the same as S0M but a relative phase angle of 180°
S1B, the same as S1M but presented binocularly
S1D, the same as S0D but with the fused dichoptic grating components at a phase angle of 180°.

Recording

Subjects were seated in a darkened radio-frequency shielded room and viewed the display through the opened door. The laboratory was dimmed to reduce distraction. VERs were recorded from a point on the scalp over the visual cortex, 2.5 cm above the inion on the mid-saggital plane with a Beckman Ag-AgCl disk electrode attached with electroconductive paste and referenced to yoked Ag-AgCl earclip electrodes; ground was established with another Ag-AgCl disk electrode on the forehead. Response signals were preamplified (0.8-50 Hz, -3 dB points) and fed to the input of a Nicolet MED-80 computer. The signals were also narrow band filtered (Krohn-hite band pass filter: 5-9 Hz) and fed simultaneously to the computer. Both raw and filtered data as well as the stimulus trigger were recorded during acquisition on FM tape (Tandberg Instrumentation Recorder) for later off-line analysis. The bandpass filter was calibrated for gain (0.9) and phase lag (106° at 7 Hz) to correct the filtered data amplitude and latency. Two stimulus shifts were recorded per averaging epoch; the time occupied by a third shift was used by the computer for artifact reject, baseline correction and variance calculations on the just completed

sweep. Thus, both "left" and "right" shifts were averaged together in the final record. Two hundred sweeps were taken per stimulus and averaged with a time resolution of 280 μsec per acquired point and a vertical resolution of 0.05 μvolts.

Analysis

Both filtered and unfiltered averaged signals were evaluated for amplitude between the most positive point following a stimulus shift (P1) and the most negative point preceding that P1 (N1). This gave two values per record for both the filtered and unfiltered signals. Latencies were calculated from the P1 and referenced to the zero crossing of the stimulus, thus giving a phase lag figure in degrees. The absolute phase lag for the visual system was calculated from the following test run, also performed at each subject-session. A sinusoidal grating at F1 was presented binocularly, and by gating the temporal waveform generator, sinusoidally counterphased six times, followed by an equivalent quiet period of time with the grating stationary. Two hundred sweeps were taken of this 1.4 second epoch. The average phase lag of the resulting six P1 peaks was taken to represent the response time of the visual system to a 7 Hz shifts/sec phase translation. The phase lag figures of the continuous stimulation runs were referenced to this lag.

DC "noise" runs showed signal to noise ratios of 2-1 or better in all subjects.

Pearson correlation coefficients were calculated between the 512 point records of all possible stimulus pairs, both filtered and unfiltered, and averaged across all subject-sessions for each stimulus. Under the assumption of linear superposition, expected response waveforms, which will be referred to as "synthetic" responses, were created by digital addition of the responses to the F1 and F3 stimulation (FSM=F1M+F3M; FSB=F1B+F3B). These synthetic responses were also compared to the observed sum of sines responses.

Unfiltered data were reacquired from tape on a long time base (1.44 sec=10 stimulus shifts per computer sweep) to avoid low frequency window effects (leakage) in the subsequent Fourier analysis. The Nyquist sample frequency cutoff was 358 Hz, which is well above the 50 Hz upper limit of the recorded data, thus preventing aliasing (Ramirez, 1974). Power spectra were calculated for each stimulus condition, and the three bins surrounding the fundamental (bin width=0.7 Hz) were summed to give the power of the VER at the stimulus frequency. The second and third harmonics were similarly quantified.

Numerical amplitude and phase data as well as the power figures and Pearson r correlation matrix were evaluated by Repeated Measures Analysis of Variance and

Duncan's Multiple Range Test by the Statistical Analysis System of the Northeast Regional Data Center.

CHAPTER V
RESULTS

Phase Calibration

Figures 3 and 4 show phase runs of two of the five subjects. Each zero-crossing of the stimulus produces a response peak that lags by at least 360° at this stimulus frequency, depending on the individual. A double response can clearly be seen in the unfiltered traces, indicating a strong second harmonic component in the response. The overall stationarity and reproducibility of the response can be seen from the grand unweighted non-normalized digital sum of all 15 subject-session phase runs in the study (Fig. 5). This method of gated stimuli permits, therefore, an absolute calibration of the phase lag in the human visual system to (quasi-) steady state stimuli, in agreement with Diamond's (1977) rejection of Regan but without his complex methodology. The values thus obtained provide the baseline latencies against which the steady-state responses are measured.

Spectral Power

The "doubling" of the response peaks to sinusoidally as opposed to abruptly (square mode) counterphasing

Figure 3. Phase run of subject A, session #1. A: unfiltered data; B: filtered data (5-9 Hz); C: counterphase trace of the grating luminance contrast; D: zero-crossing signal. The numbers between C and D indicate stimulus events; the numbers over the peaks in A and B indicate the respective response positivities.

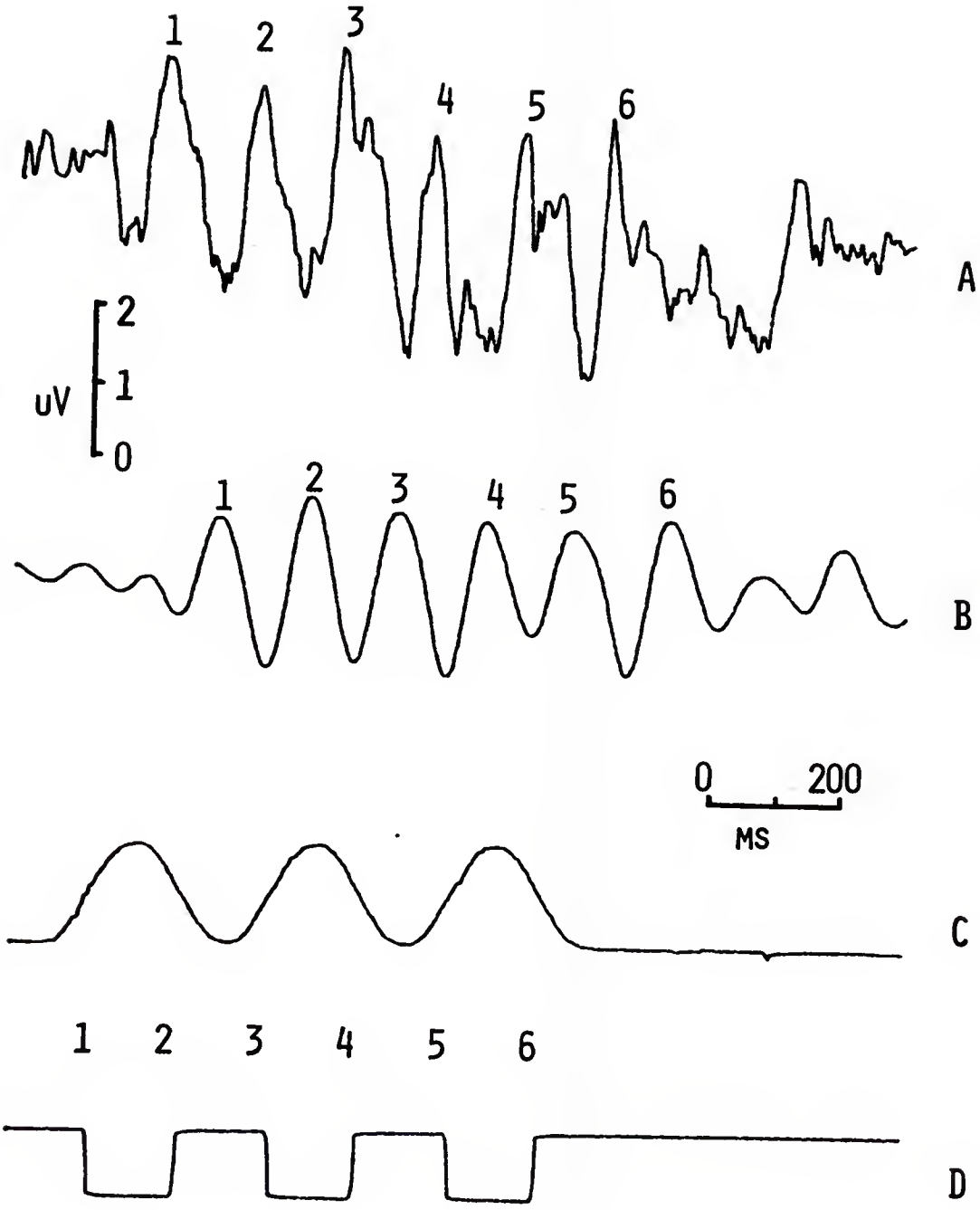

1
2
3
4
5
6
A
uV
2
1
0
1
2
3
4
5
6
B
0
200
MS
C
1
2
3
4
5
6
D

Figure 4. Phase run of subject B, session #3. Otherwise as in Fig. 3.

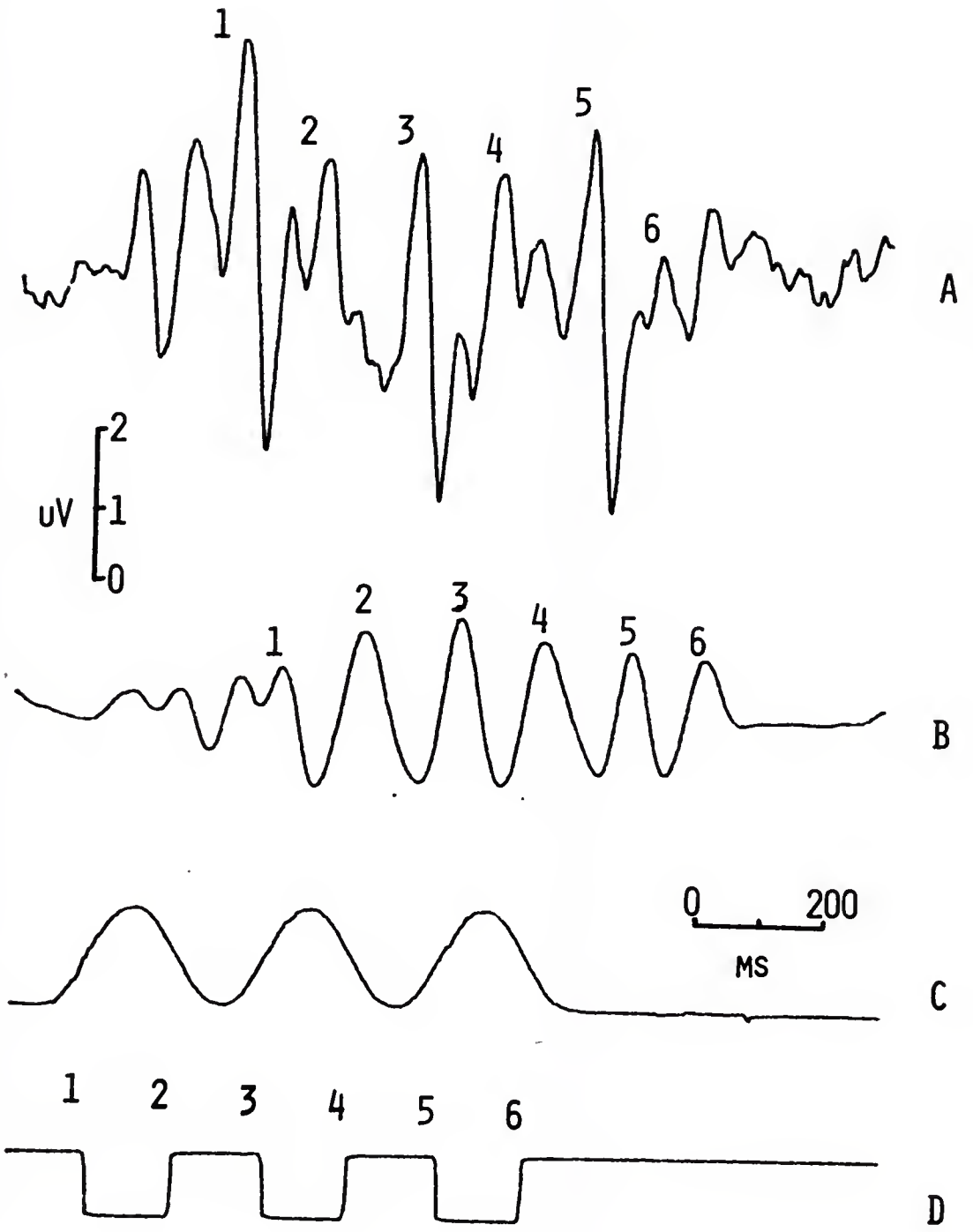
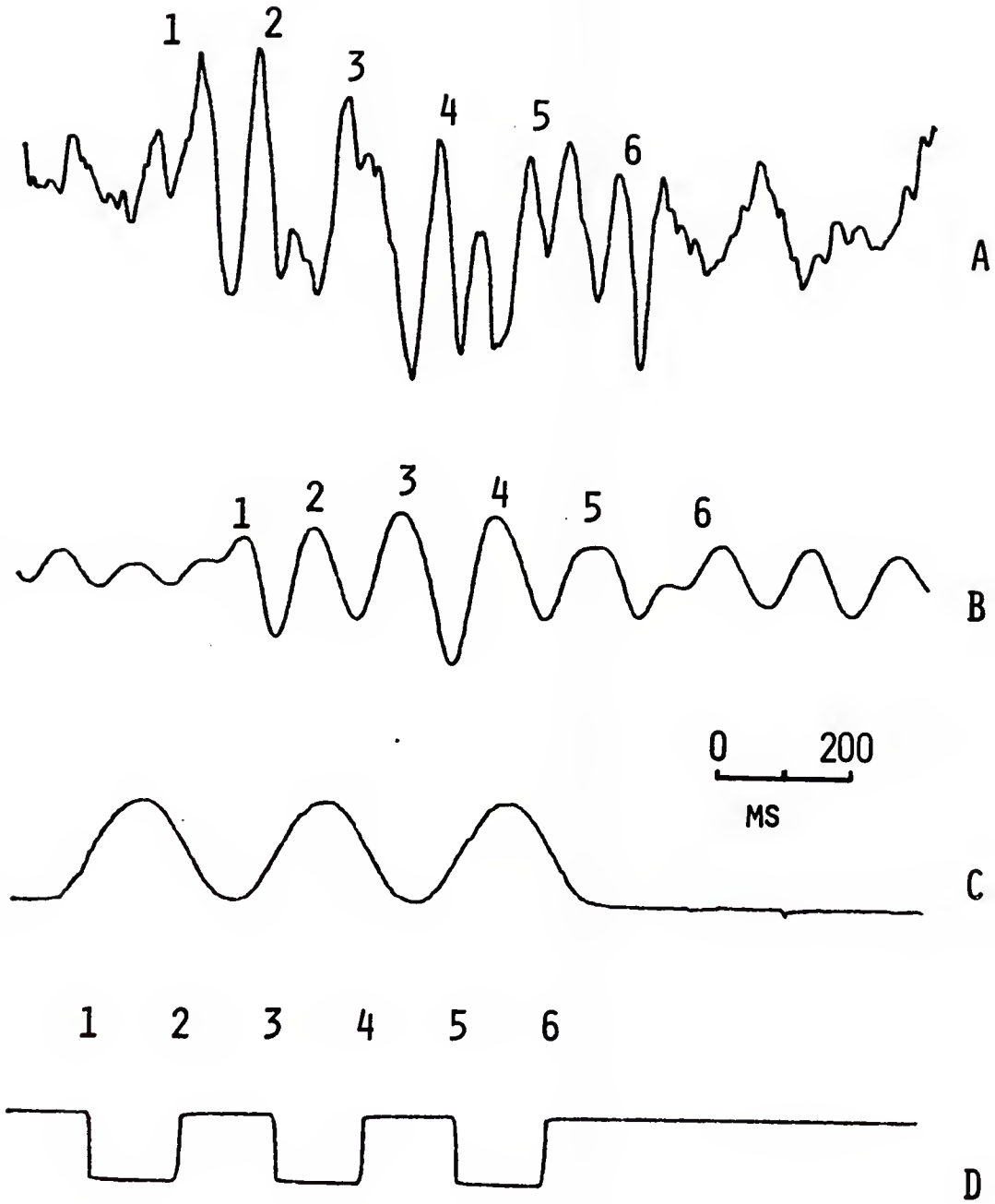

1
2
3
4
5
6
A
uV
2
1
0
1
2
3
4
5
6
B
0
200
MS
C
1
2
3
4
5
6
D

Figure 5. Grand unweighted, non-normalized digital sum of all 15 subject-session phase runs. Otherwise as in Fig. 3. Absolute amplitude is arbitrary.


1
2
3
4
5
6
A
1
2
3
4
5
6
B
0
200
MS
C
1
2
3
4
5
6
D

stimuli can be seen to occur in monocular, binocular and dichoptic presentations, whether of simple or complex gratings (Figs. 6, 7, 8 and 9). The enhancement of the second harmonic by the sinusoidal mode can be clearly seen in the power spectra of each response.

Means of the fundamental and second harmonic power are graphed in Fig. 10; their ratios in Fig. 11. Statistical analysis showed that for square mode counterphasing stimuli, the fundamental frequency of the response is greater than the second harmonic ($p=0.0016$) for all stimuli, but that the fundamental and second harmonic are not significantly different in the sinusoidal case ($p>0.05$ by Duncan's). The third harmonic showed essentially no mode or stimulus differences. The analysis of the frequency component power ratios confirmed this, but the large variability of the non-normalized data allowed only four of the 10 stimuli (F1M, S1B, S0B and S0M) to show a significant mode difference ($p<0.05$, SQ>SN) although all the others also tended in the same direction. The response power of all stimuli showed overlapping ranges by Duncan's test in the sine mode, but S0M proved a significantly higher fundamental to second harmonic power ratio in the square mode presentation than all other stimuli (see below).

Analysis of the monocular vs binocular subsets of the power data for "simple" gratings (F1M, F1B, F3M, F3B) showed no significant differences in the fundamental,

Figure 6. Responses to a monocular presentation of a complex grating with the components at a phase angle of 0°. A: unfiltered data; B: filtered data; C: stimulus traces (sine or square mode counterphase) as well as time and amplitude calibration on square wave; D: power spectra of responses. Note a factor of two scale shift of the sine mode versus square mode power spectra.

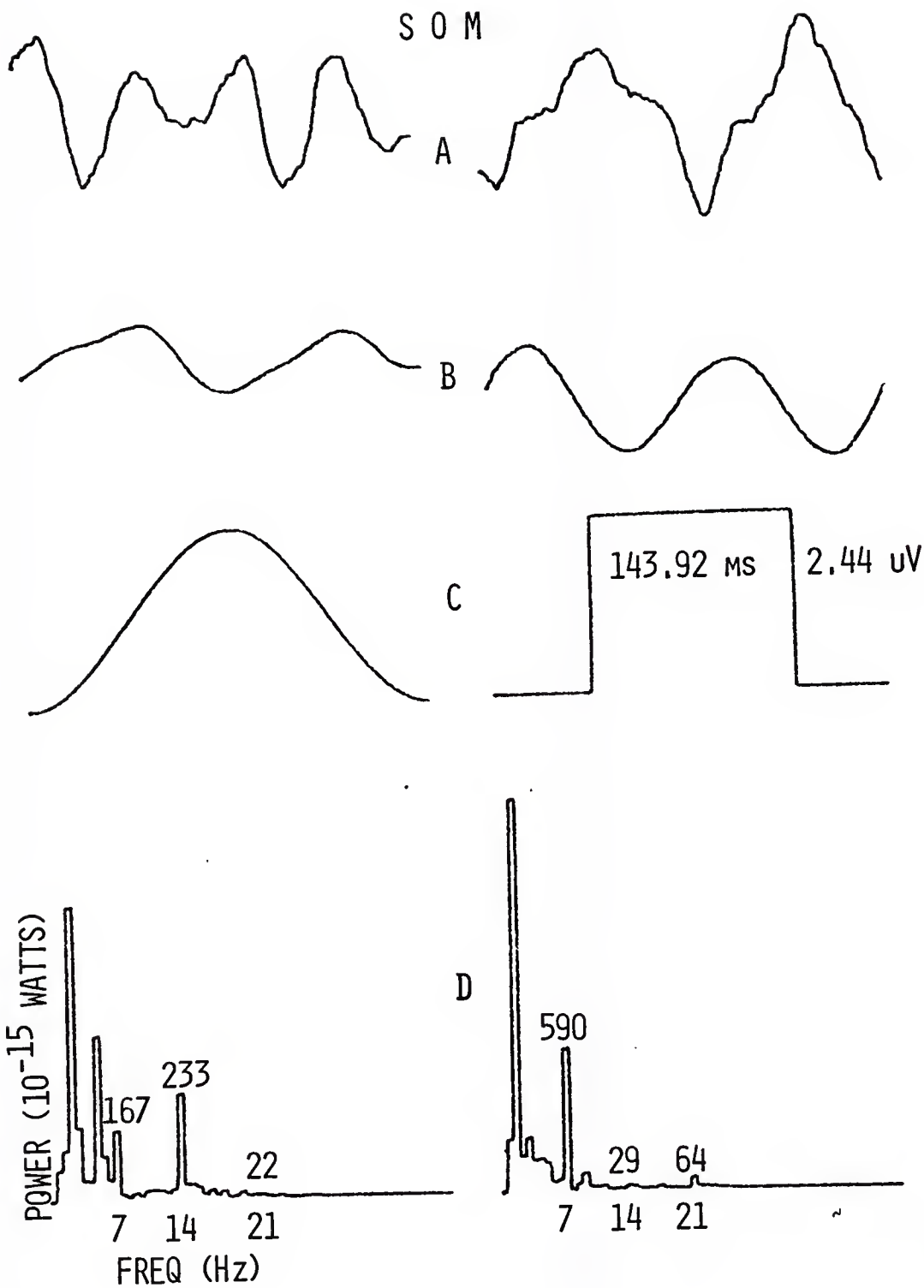

S O M
A
B
C
143.92 ms
2.44 uV
D
POWER (10^{-15} WATTS)
167
233
22
7
14
21
FREQ (Hz)
590
29
64
7
14
21

Figure 7. Responses to a binocular presentation of a complex grating with the components at a phase angle of 0^{o}. Otherwise as in Fig. 6.

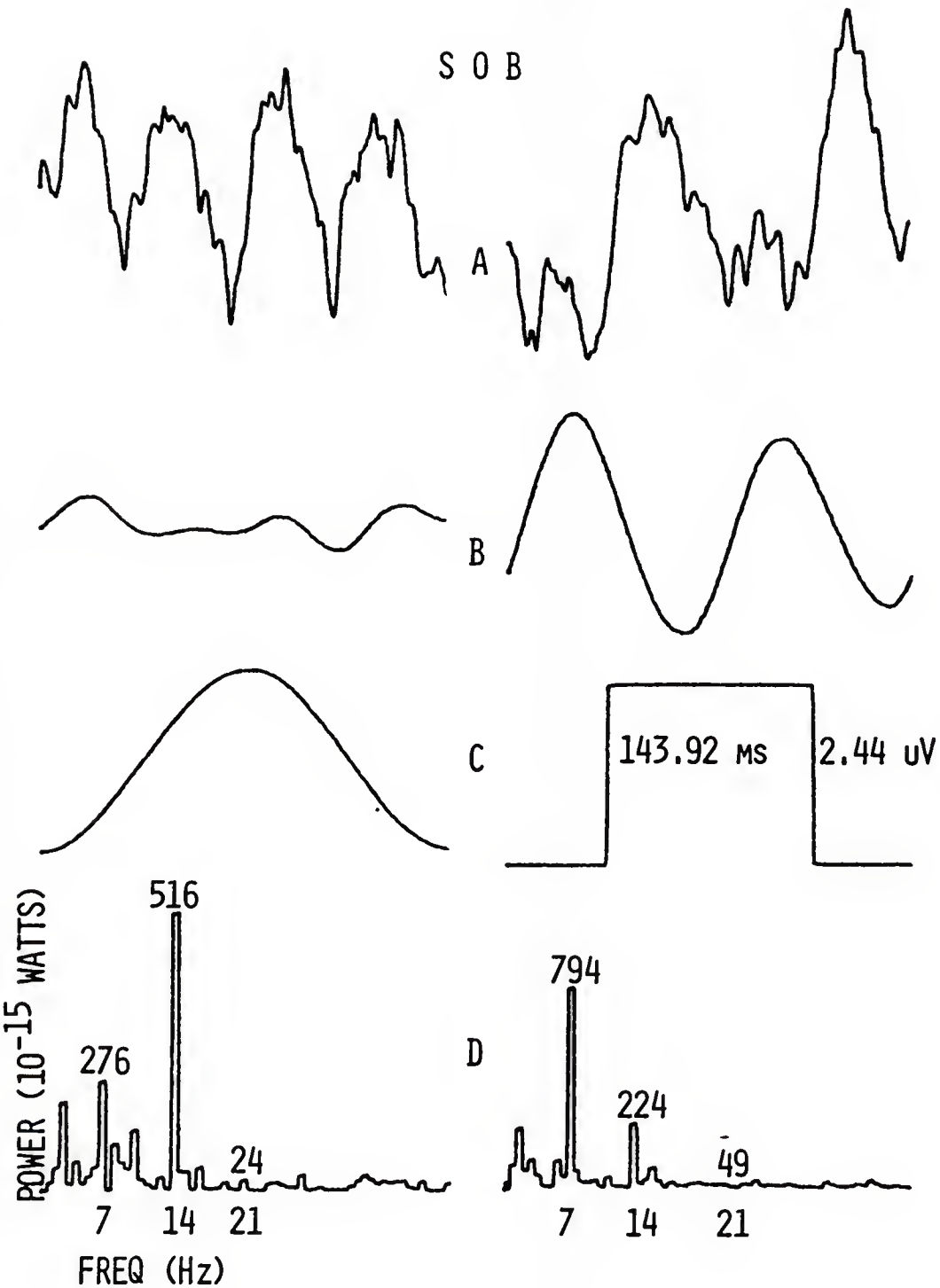

S O B
A
B
C
143.92 ms
2.44 uV
D
516
276
24
794
224
49
POWER (10^{-15} WATTS)
7
14
21
FREQ (Hz)

Figure 8. Responses to a binocular presentation of a simple (F1: 2 cycles/degree) grating. Otherwise as in Fig. 6.

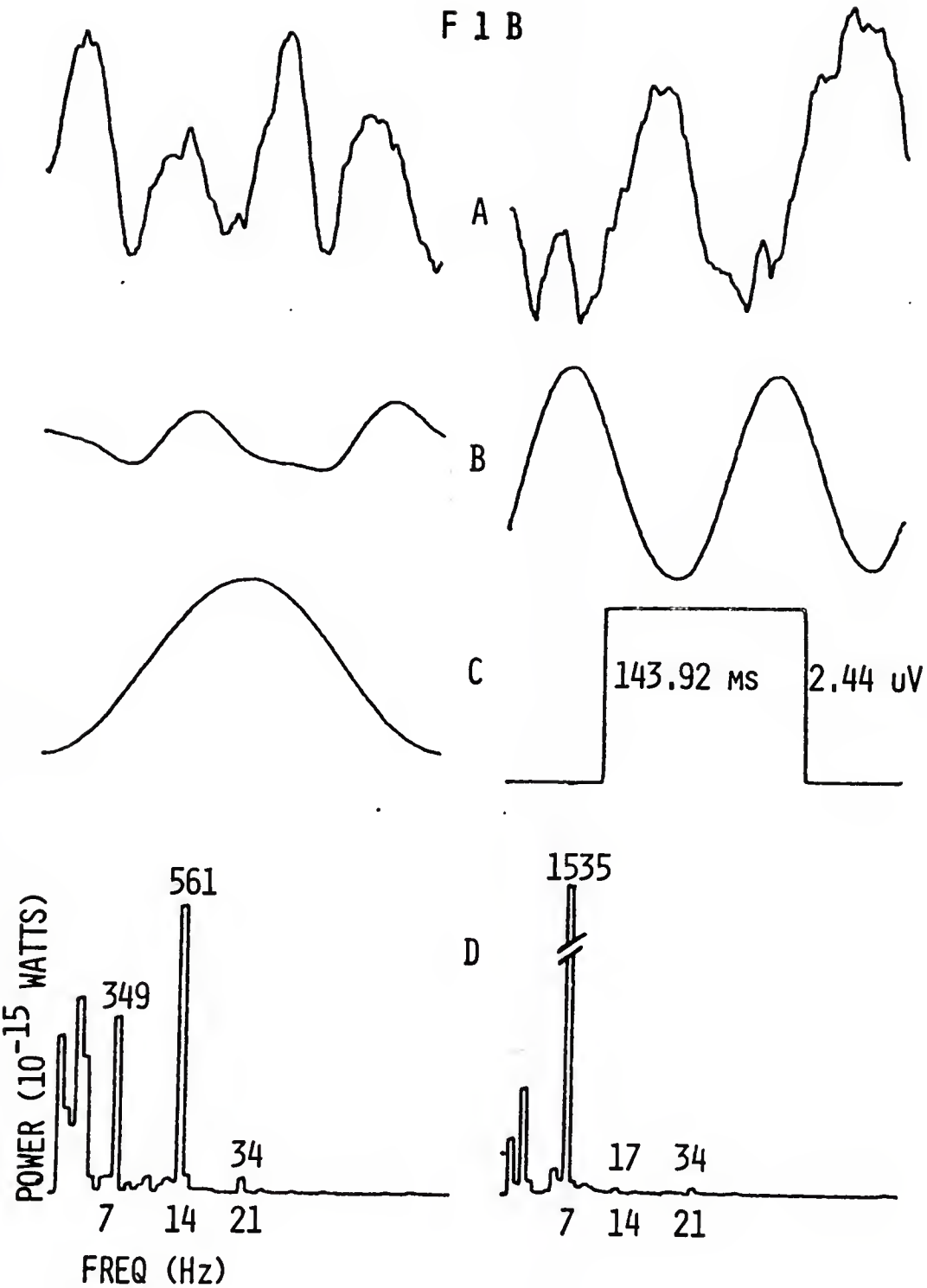
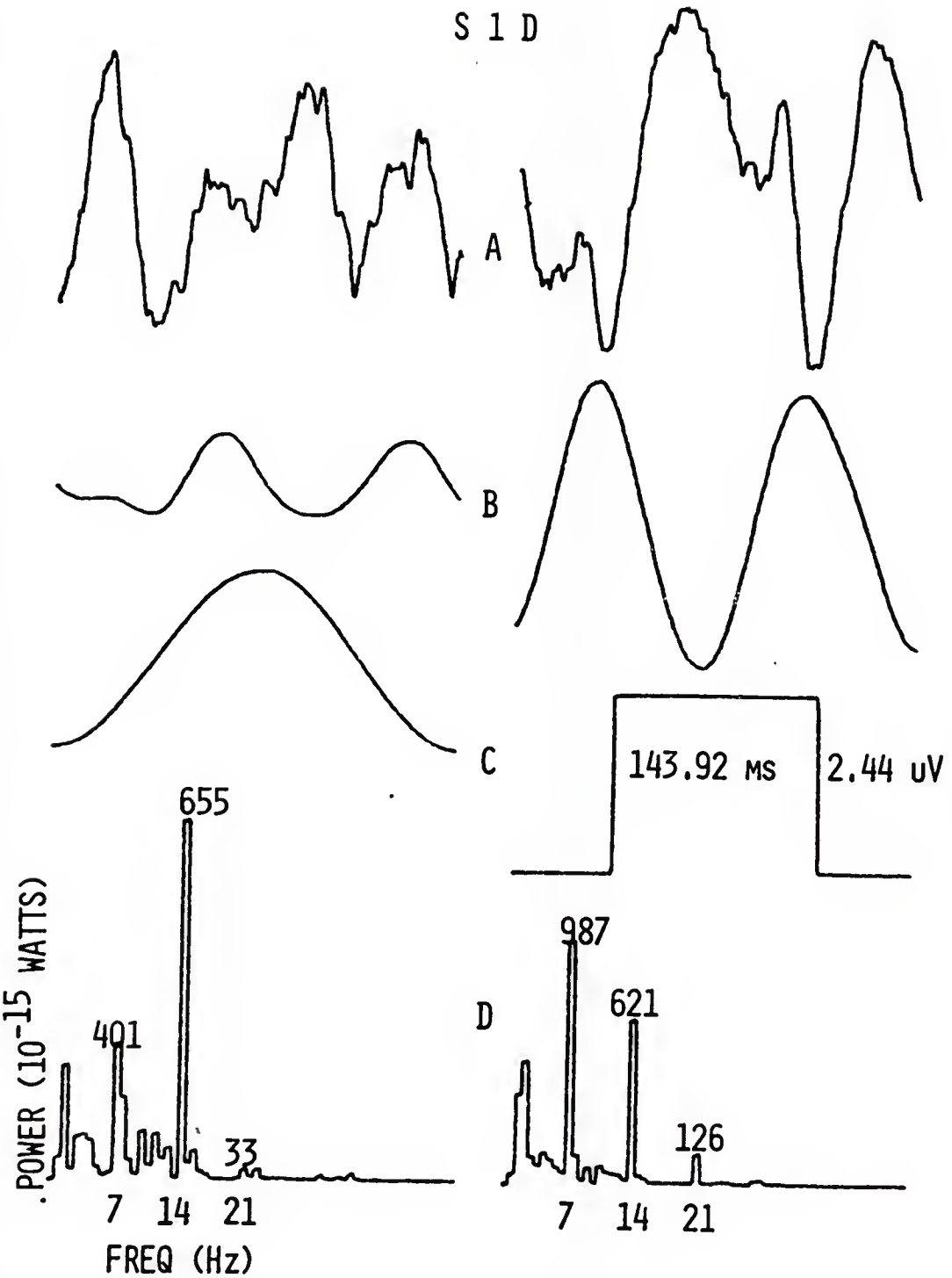

F 1 B
A
B
C
143.92 ms
2.44 uV
D
561
349
34
1535
17
34
7
14
21
7
14
21
POWER (10^{-15} WATTS)
FREQ (Hz)

Figure 9. Responses to a dichoptically presented gratings (F1+F3) with the components at a phase angle of 180°. Otherwise as in Fig. 6.


S 1 D
A
B
C
143.92 ms
2.44 uV
655
401
33
POWER (10^{-15} WATTS)
7 14 21
FREQ (Hz)
D
987
621
126
7 14 21

second harmonic or their ratio in either sine or square modes. For the complex stimuli (S0M, S0B, S0D, S1M, S1B, S1D), the fundamentals were not significantly different ($p>0.05$) but the second harmonic showed a significant difference due to condition ($p=0.0074$); i.e., binocular and dichoptic values are both significantly above monocular values. The frequency component ratio showed complex interactional effects (phase by condition by mode: $p=0.0002$); however, the pattern of significances in the breakdown showed merely that monocular ratios tended to be greater than binocular and dichoptic ratios, and that square mode ratios tended to be greater than sine mode ratios, echoing the earlier analysis. Also, a significant difference due to component phase appeared in the square mode monocular power ratio ($p=0.0049$) indicating that complex stimuli with a phase angle of 0^{o} between the first and third harmonic components (S0M) show a higher temporal response component power ratio (fundamental/second harmonic) than with a phase angle of 180^{o} (S1M), i.e., an enhancement of the fundamental compared to the second harmonic when the components are in a square wave phase relationship; but as neither component alone is significantly affected, the significance of this result remains unclear.

Figure 10. Bar graph of response power to component fundamental (F1) and second harmonic (F2) by mode sine (SN) and square (SQ) mode counterphase and stimulus; means and standard error of the means (n=15)

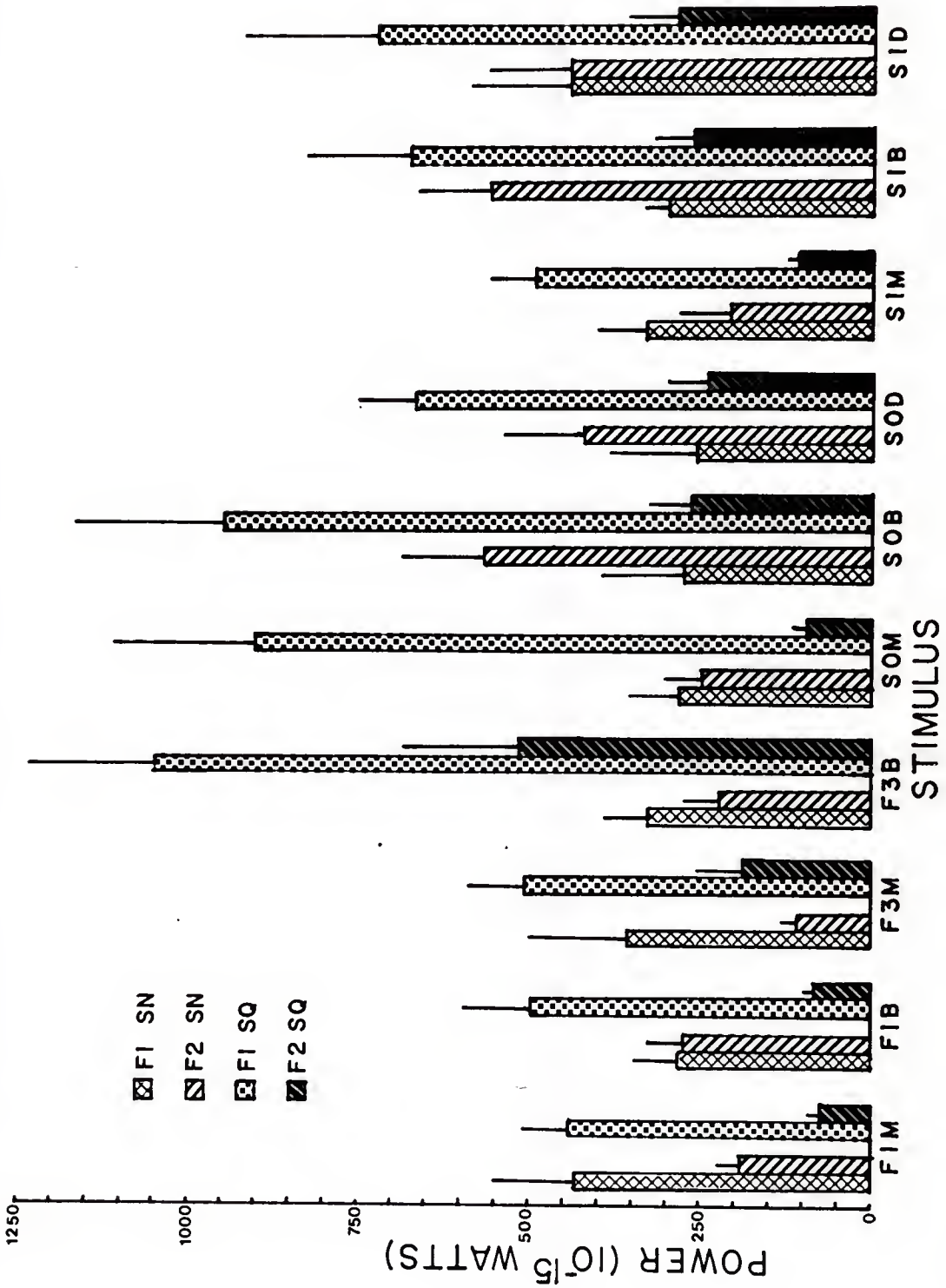
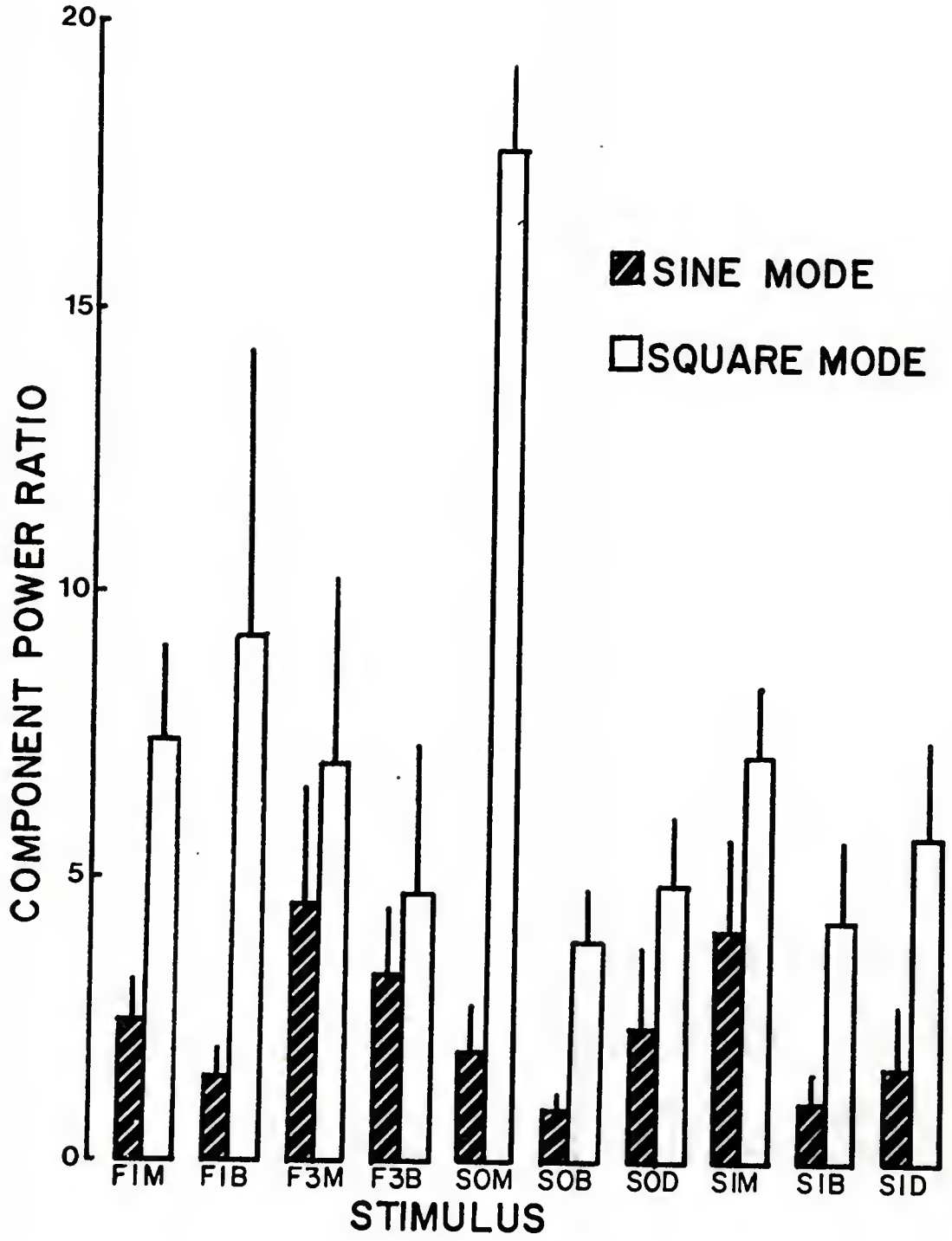

F1 SN
F2 SN
F1 SQ
F2 SQ
F1M
F1B
F3M
F3B
SOM
SOB
SOD
SIM
SIB
SID
STIMULUS
POWER (10⁻¹⁵ WATTS)
0
250
500
750
1000
1250

Figure 11. Bar graph of the component power ratio (fundamental/second harmonic) by mode and stimulus. Means and standard error of the means (n=15).


20
15
10
5
0
COMPONENT POWER RATIO
SINE MODE
SQUARE MODE
F1M
F1B
F3M
F3B
SOM
SOB
SOD
SIM
SIB
SID
STIMULUS

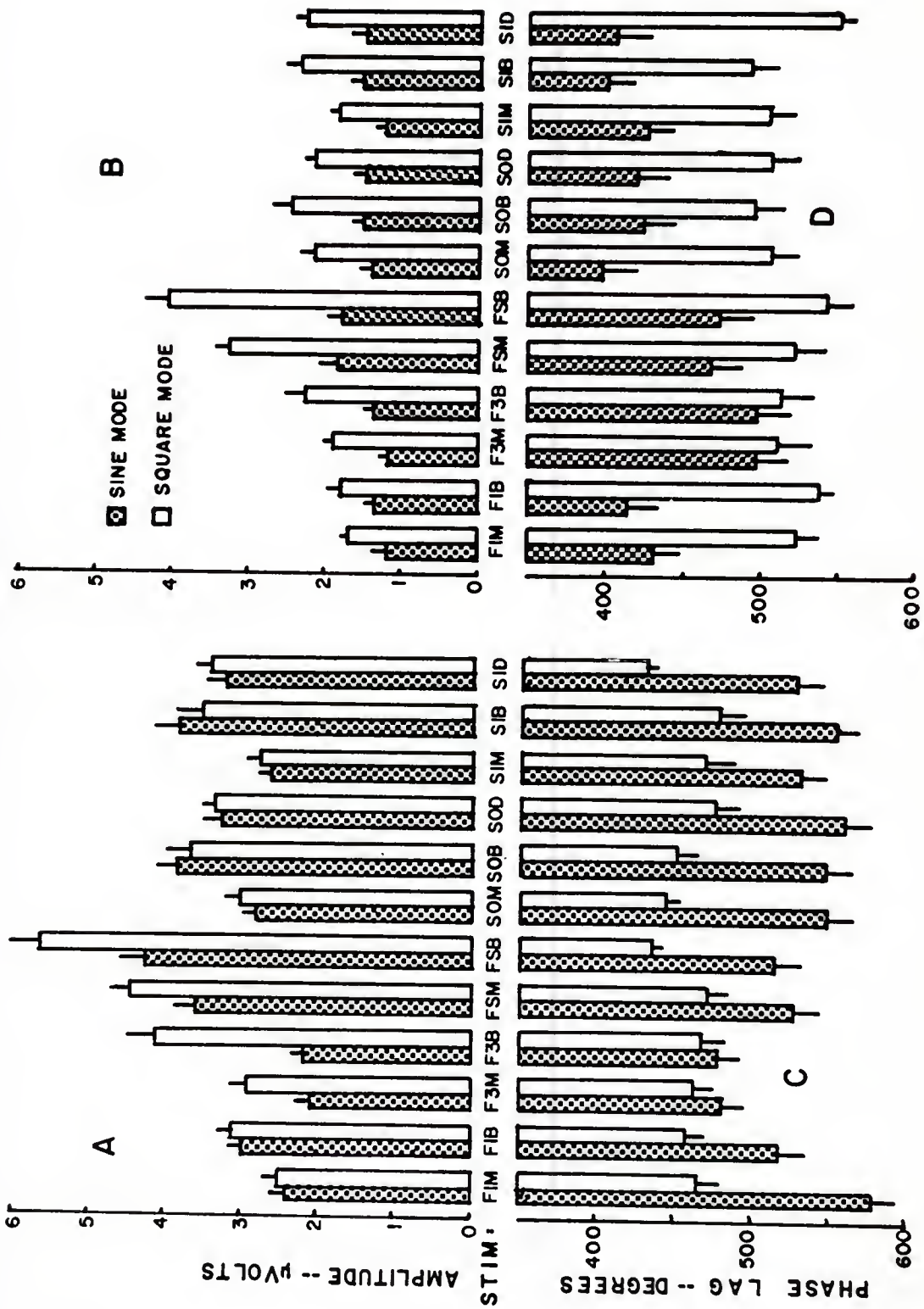
Amplitude Analyses

The mean unfiltered and filtered response amplitude values are graphed in Figs. 12 A and B for all stimuli as well as for the synthetic responses. Immediately apparent is that the synthetic binocular sum (FSB) is significantly higher than all other stimuli in both sine and square modes, unfiltered, and in the filtered square mode (all p's=0.0001); the filtered sine mode values showed no significant ranking of stimuli ($p=0.5142$). Actual responses to complex (sum of sinusoid) gratings tended to cluster in the center of the ranking and indicate that the response to input on "separate" spatial frequency channels is in general not a linear addition of the responses to the components presented separately. Relative stimulus component phase angle had no significant effect on the response metrics.

With one exception (F3M), square and sine mode unfiltered amplitudes do not differ significantly; square mode responses tend to be larger than sine mode responses in the filtered case but not strongly so ($p<0.05$ in F3B, F3M and S1M; other stimuli rank square>sine but have $p<0.05$). Also as expected, unfiltered data tend to be larger than filtered data for all modes and stimuli ($p<0.05$).

Rearranging the amplitude data for simple gratings into subsets, the responses to F1 and F3 grating stimuli (2 and 6 cycles/degree) do not differ significantly;

Figure 12. A: means and standard error of the means of response amplitude, both sine and square mode, by stimulus: unfiltered data; B: filtered data; C: means and standard error of the means of response phase, unfiltered data; D: filtered data (n=30).


A
B
C
D
AMPLITUDE -- μVOLTS
PHASE LAG -- DEGREES
STIM:
FIM FIB F3M F3B FSM FSB SOM SOB SOD SIM SIB SID
SINE MODE
SQUARE MODE
0 1 2 3 4 5 6
400 500 600

however, they are both less than the synthetic responses (FSM and FSB: $p=0.0001$ for monocular, $p=0.0003$ for binocular conditions). For all stimulus frequencies (F1, F3 and FS) and both modes (sine and square), binocular responses were higher than monocular but not significantly so ($0.18>p>0.05$). With complex stimuli (S0 and S1), the sine mode unfiltered responses did show a significant ranking ($p=0.0148$: binocular>dichoptic>monocular, with overlapping Duncan's ranges), which was weakly confirmed with the square mode responses ($p=0.0709$). This indicates that the monocular response is not depressed by "masking" in the fellow eye when the "mask" is of a (square wave) harmonically related frequency but rather the response is enhanced to fall between monocular and binocular levels.

Phase Analyses

Figures 12 C and D show the phase values of the filtered and unfiltered responses respectively. In general, the square mode phase is unaffected by filtering ($p=0.2220$), whereas the sine mode is, although the difference reaches significant levels for only two stimuli (F1M and S1B, $p<0.05$: unfiltered>filtered); the other stimuli follow the same pattern. Also, in general, the trend is for unfiltered sine mode responses to have larger, i.e., longer phase lags than square mode ($p=0.0772$) whereas the opposite holds true for filtered responses (mode by stimulus: $p=0.0228$; S1D and S1M:

$p<0.05$, square>sine; other stimuli nonsignificant but in the same pattern). The differences are due to the separate phase of the second harmonic in the sine case. The stimuli did not rank in any significant order as the Duncan's ranges overlapped extensively. Grouping the data by condition (monocular, binocular and dichoptic) also revealed no significant relationships.

Correlation Analysis

Pearson correlation coefficients were calculated between all possible response pairs for each subject session, both filtered and unfiltered, to define a data base for comparing individual mean correlations to the general mean. A selection of mean correlations across subject-session comparing the synthetic sum of spatial frequency responses to the actual responses is given in Table 1. Of the entire matrix of 276 mean correlations of unfiltered responses, only the correlation of FSB-SQ vs SlD-SQ (unfiltered) fell more than one standard deviation above the mean (neglecting the trivial correlations of e.g., FlM with FSM, as FlM+F3M=FSM). None of the 276 filtered data correlations fell above one standard deviation over the mean. The analysis of variance on the matrices indicated that the ranking of correlations was significant ($p=0.0001$ for both filtered and unfiltered cases), but all the Duncan's ranges overlapped extensively. However, even in this one case, only 61% of

Table 1. Selected Pearson Correlation Coefficients comparing synthetic sum of component grating responses (FSM and FSB) to actual responses (S0M, S0B, S0D, S1M, S1B, S1D); U: unfiltered; F: filtered data; SN: sine mode; SQ: square mode.

FSM		FSB				
SN	SQ	SN	SQ			
.5102	.1620	.5032	.1969	U	SN	S0M
.5853	.2273	.4608	.2633	F		
.2814	.6701	.2149	.7003	U	SQ	
.3985	.8673	.3390	.8318	F		
.4362	.1656	.5883	.2121	U	SN	S0B
.4544	.2292	.6227	.2424	F		
.3493	.5792	.3898	.6255	U	SQ	
.2984	.7409	.3267	.7316	F		
.4424	.2237	.4470	.1674	U	SN	S1M
.4925	.2007	.3424	.1438	F		
.3559	.6205	.2595	.5762	U	SQ	
.4299	.7716	.2273	.7063	F		
.4713	.0450	.5513	.1057	U	SN	S1B
.3149	-.0530	.4418	-.0636	F		
.3222	.5942	.2804	.6270	U	SQ	
.2148	.6561	.2985	.6526	F		
.5227	.2675	.5523	.2562	U	SN	S0D
.6388	.2522	.4952	.2329	F		
.4125	.6514	.4444	.6462	U	SQ	
.5501	.8905	.4560	.7904	F		
.4821	.2889	.5554	.3580	U	SN	S1D
.3868	.2581	.4477	.2962	F		
.4827	.7231	.4324	.7833	U	SQ	
.4928	.9191	.3951	.9336	F		

	Mean	S.D.	Mean + S.D.	Mean - S.D.
U:	.3830	.3599	.7429	.0231
F:	.4047	.5803	.9850	-.1756

the variance in the observed dichoptic sum of spatial frequencies response is accounted for by the individual responses to the single spatial frequencies. This indicates a definite nonlinearity, i.e., interaction, at suprathreshold levels, between these spatial frequency channels.

Results Summary

In short, therefore, the power spectral analysis has shown a significant enhancement of the second temporal harmonic component of the evoked waveform to the sinusoidal counterphase mode of stimulation. The amplitude analysis has refuted the concept of a linear superposition of spatial frequency channels greater than one octave apart. The phase analysis shows complex effects that are not easily relatable to either stimulation mode or spatial stimulus waveform. Lastly, the correlation analysis has shown a partial prediction of the response waveforms to complex grating stimulation by the summed responses to their simpler components, that does not depend on eye-of-origin information.

CHAPTER VI
DISCUSSION

Sinusoidally counterphased gratings physically present stimulus power at only one temporal frequency. Abrupt counterphasing presents energy at all the odd harmonics of the fundamental as well. Thus, square wave counterphased gratings, having only one stimulus event per shift, will necessarily show power in the fundamental frequency in the response waveform, and may show power in the odd harmonics as well. Regrettably, whether the third harmonic of the stimulus is also generating a response waveform, the non-normalized data are too variable to show. The unexpected finding of peak splitting of the response waveform to sinusoidal stimulation, however, indicates that the visual system is not responding in a linear fashion in the temporal domain. An explanation can be proposed based on the contrast sensitivity curve, namely that the grating is not being perceived as counterphasing, but rather that two separate gratings are alternately appearing and vanishing, with each onset into visibility and offset into the period of perceived "non-grating" mean luminance acting as a stimulus event and generating its own peak (Spekreijse, van der Tweel and Zuidema, 1973). This would explain the appearance of a

"second harmonic" to the presumed stimulation frequency. An alternative explanation could be proposed from the observation that a sinusoidally counterphasing grating can be decomposed into two gratings drifting across one another (Sekuler, Pantle and Levinson, 1978). This would require the hypothesis that the mechanism responding to e.g., the rightward drifting grating respond with a different latency to that responding to the leftward drifting grating; however, such differential directional responses have not been noted in the evoked potential literature, unlike spatial frequency differences which do correlate with latency changes (Vassilev and Strashimirov, 1979).

Channel independence in the spatial frequency domain assumes independently responding mechanisms, and thus, presumably, independent evoked responses. Psychophysical masking experiments have postulated a destructive interaction between channels that suppresses the response below monocular levels in a dichoptic paradigm; however, the data reported here support neither of these two positions. If the two and six cycles/degree channels were independent, the digital sum of the monocular responses would be of the same amplitude and phase as well as highly correlated with the observed dichoptic sum of gratings response. The dichoptic response not only is lower than the synthetic response whether monocular or binocular, indicating some occlusion, but the correlation

coefficients are also low (see Table 1), for example, FSM/SOD, square mode, unfiltered, shows only 43% of the variance accounted for. The filtered cases, of course, have higher values, but even with the data reduced to the response fundamental, only 79% of the variance is accounted for. Neither of these values falls more than one standard deviation above the mean correlation of the entire data matrix, and therefore is of doubtful significance. But it is also clear that a suppression of the evoked potential by the dichoptic condition did not occur either. Separate channels are still, however, a valid model of some of the data, since the relative phase angle of the stimulus components does not affect the response fundamental or amplitude, despite a 10% difference in overall contrast. What remains, therefore, is that in the steady-state, suprathreshold case, gratings that are square wave related, i.e., in a 1:3 harmonic relationship, and phase locked, do interact and enhance the evoked potential approximately 15% above the monoptic case but not to the level of the pure binocular stimulation response (approximately 24%).

Comparing the responses to two-spatial-frequency-channel-stimulation by condition of stimulus (monoptic vs. dichoptic) leads to evidence suggesting the site of interaction of these channels. The data for simple gratings showed a small, if non-significant, binocular versus monocular enhancement (approximately 17%),

presumably explained by the fact that the monocular case in this study was quasi-binocular. There was always the same total luminance field presented to each eye at all times, rather than a dark field to one eye as in classical binocular facilitation studies which demonstrate 1.4 fold enhancement. Thus, one can assume that at least some aspects of the binocular mechanisms were also activated in the "monocular" case, i.e., the various conditions of stimulus presentation did not radically alter the responding population of cortical neurons giving rise to the evoked signal. If the interaction between the two and six cycle/degree channels is cortical, the cortical population of neurons can "see" a difference between the monoptic and dichoptic sum of gratings only with a monocular suppression (or by integrating the information from purely monocular cells), not otherwise (Braccini, Gambardella and Suetta, 1980). This implies that S0M=S0D and S1M=S1D in the fused case. On the other hand, if the interaction is precortical, i.e., before integration of information of the two eyes, not only would FSM=S0D, but S0M≠S0D. Since the Duncan's ranges showed a monocular and dichoptic overlap in agreement with Sturr and Teller's (1973) dichoptic disk/anulus sensitization experiments (as well as a binocular-dichoptic overlap), none of the conditions for a precortical locus are satisfied, whereas those for a cortical one are. Additionally, eye-of-origin information does not appear to be an important

characteristic of spatial frequency channels when examined with an equal-luminance paradigm.

APPENDIX
CIRCUIT DESCRIPTION AND PARTS LIST

The circuit diagrammed in Fig. 13 consists of four major sections:

1. a fundamental plus third harmonic spatial waveform synthesizer,

2. a logic switch pair to abruptly replace this waveform with its inverse

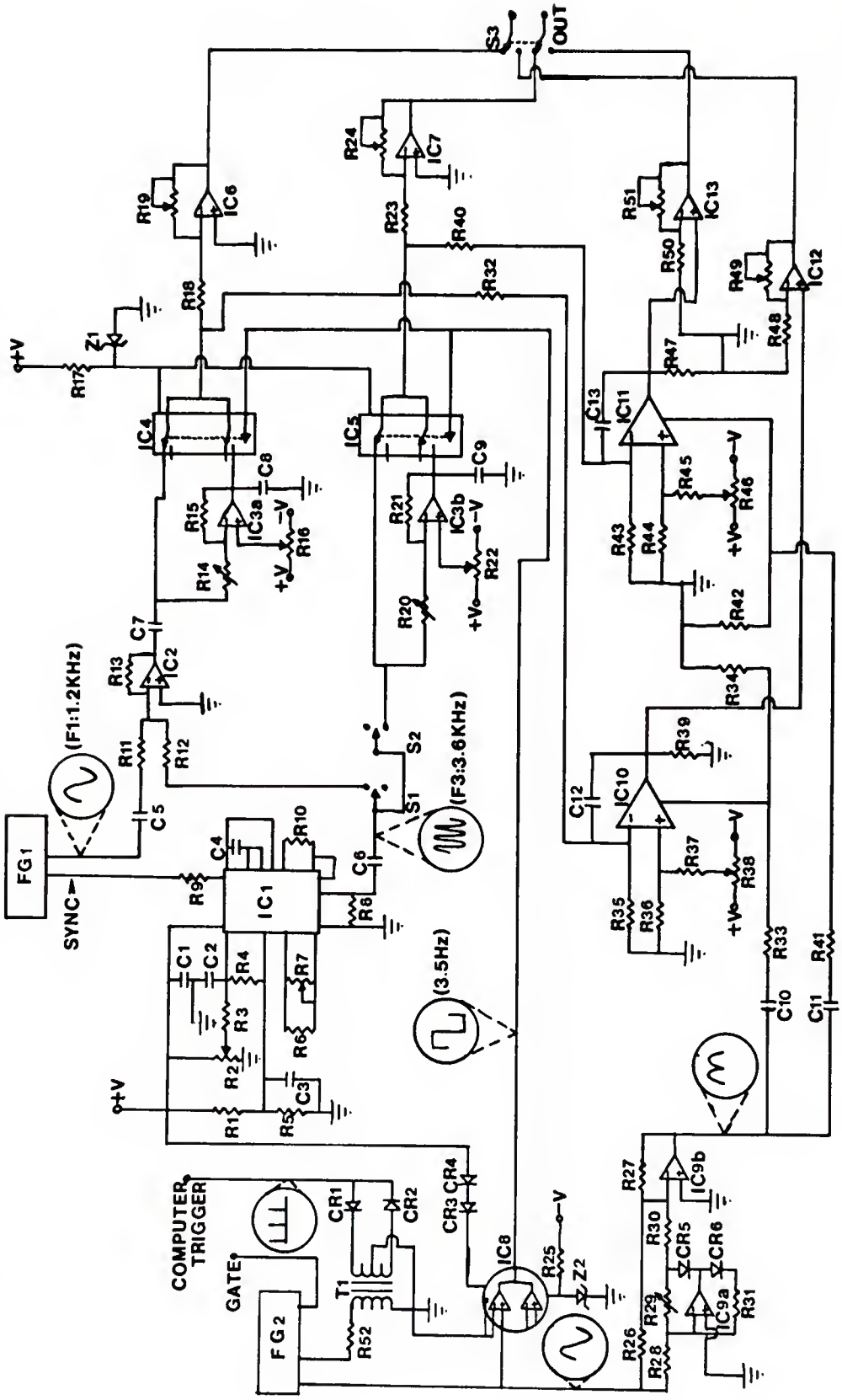
3. a temporal waveform synchronizer, and

4. a programmable variable gain amplifier for amplitude modulation.

The first section consists of FG1, IC1 and IC2 with their associated discrete components. The F3 frequency is set by C4, and FG1 is tuned to 1/3 this value. The SYNC pulse from FG1 locks the peaks of the two waveforms together. Phase selectivity (0^{o} or 180^{o}) is determined by which SYNC pulse (peak or valley) is seen by IC1. Switches S1 and S2 determine whether a composite waveform (F1+F3=Σ) is seen by the remainder of the circuit, or only the simple waveforms.

The second section (ICs 3-7) creates the inverted waveforms, and in response to IC8's output, switches between them and the noninverted signals. Final gain adjustment for the square wave mode counterphase output is accomplished by ICs 6 and 7.

Figure 13. Schematic diagram of the stimulus circuitry labelled "ST" in Fig. 1.


S3
OUT
R24
IC7
R23
R40
R32
R19
IC6
R18
Z1
+V
R17
IC4
IC5
C8
C9
R15
IC3a
-V
R16
+V
R14
R21
IC3b
-V
R22
+Vo
R20
C7
R13
IC2
R11
R12
C5
(F1:1.2KHz)
FG1
SYNC
S2
S1
(F3:3.6KHz)
C4
R10
C6
R9
IC1
R6
C1
C2
R4
R3
R7
R6
R2
C3
R1
R5
+V
(3.5Hz)
R51
IC13
R50
R49
IC12
R48
R47
C13
IC11
R45
R46
+Vo
-V
R43
R44
R42
R34
R39
C12
IC10
R37
R38
+Vo
-V
R35
R36
R33
R41
C10
C11
COMPUTER TRIGGER
GATE
FG2
CR1
CR2
CR3
CR4
T1
R52
IC8
R25
Z2
-V
R27
IC9b
R30
CR5
CR6
R29
IC9a
R31
R26
R28

The third section has two parts: a zero-crossing detector (IC8) and an ideal rectifier (IC9). The input waveform comes from FG2 and determines the counterphase rate as well as the programming waveform for the last stage. FG2 also produces a square wave, synched to its sine wave output, to generate a computer trigger pulse through T1, CR1 and CR2.

The final stage (ICs 10-13) takes the rectified temporal signal to control the gain of the square wave mode counterphasing signal of section two and sinusoidally varies the amplitude. As the TTL switches are counterphasing at the zero-crossing of the temporal waveform from FG2, the output will change phase by 180° at that point at which the instantaneous output voltage from ICs 10 and 11 are zero. This produces the sine-mode counterphased signal.

Square- and sine-mode outputs are selected by S3 and fed to the Z-axes of the two oscilloscopes comprising the stimulus display.

Voltage Regulators

Z1	1N761A	4.9 V zeener diode
Z2	1N754Z	6.8 V zeener diode

Current Regulators

CR1	SA 1181/631-1	Diode
CR2	SA 1181/631-1	Diode
CR3	1N4067	Diode
CR4	1N4067	Diode
CR5	1N4146	Diode
CR6	1N4148	Diode

External Units

FG1	WAVETEC model 110	Function generator
FG2	EXACT model 505	Function generator
+V/-V	Power supply	(+15 volts/-15 volts)

Switches

S1	DPST	Slide switch
S2	DPST	Slide switch
S3	DPDT	Toggle switch

Integrated Circuits

IC1	XR205	Function generator
IC2	741	Op amp
IC3a	1/2 747	Op amp
IC3b	1/2 747	Op amp
IC4	LH5042	TTL DPDT switch
IC5	LH5042	TTL DPDT switch
IC6	741	Op amp
IC7	741	Op amp
IC8	LH711	Dual comparator
IC9a	1/2 747	Op amp
IC9b	1/2 747	Op amp
IC10	CA3090	Transconductance amp
IC11	CA3090	Transconductance amp
IC12	741	Op amp
IC13	741	Op amp

Transformer

T1	--	Audio transformer

Capacitors

C1	0.1	microfarad
C2	0.1	microfarad
C3	0.1	microfarad
C4	0.01	microfarad
C5	0.1	microfarad
C6	0.1	microfarad
C7	0.1	microfarad
C8	300	picofarad
C9	300	picofarad
C10	4.7	microfarad
C11	4.7	microfarad
C12	300	picofarad
C13	300	picofarad

Resistors (Values in Ohms)

R1	10K	
R2	20K	Trim pot
R3	10K	
R4	5K	
R6	4K	
R7	5K	Trim pot
R8	1K	
R9	1K	
R10	15K	
R11	10K	
R12	10K	
R13	10K	
R14	5K	Trim pot
R15	5K	
R16	200K	Balance pot
R17	220	
R18	5K	
R19	5K	Trim pot
R20	5K	Trim pot
R21	5K	
R22	200K	Balance pot
R23	5K	
R24	5K	Trim pot
R25	220	
R26	10K	
R27	33K	
R28	5K	
R29	5K	Trim pot
R30	5K	
R31	5K	
R32	4.7K	
R33	18K	
R34	27K	
R35	47K	
R36	47K	
R37	47K	
R38	50K	Balance pot
R39	2.37K	
R40	4.7K	
R41	18K	
R42	27K	
R43	47K	
R44	47K	
R45	47K	
R46	50K	Balance pot
R47	2.3K	
R48	5K	
R49	5K	Trim pot
R50	5K	
R51	5K	Trim pot
R52	100	

LITERATURE CITED

Abadi R.V. (1976) Induction masking--A study of some inhibitory interactions during dichoptic viewing. Vision Res. 16, 169-175.

Abadi R.V. and Kulikowski J.J. (1973) Linear summation of spatial harmonics in human vision. Vision Res. 13, 1625-1628.

Abel L.A. and Quick Jr. R.G. (1978) Wiener analysis of grating contrast judgments. Vision Res. 18, 1031-1039.

Adachi-Usami E. (1979) Comparison of contrast thresholds of large bars and checks measured by VECPs and psychophysically as a function of defocusing. Albrecht v. Graefes Arch. klin. exp. Ophthal. 212, 1-9.

Albrecht D.G., DeValois R.L. and Thorell L.G. (1979) Visual cortical neurons: Are bars or gratings the optimal stimuli? Science 207, 88-90.

Andreassi J.L., Zalkind S.S., Galichio, J.A. and Young N.E. (1979) Monocular and binocular visual evoked potentials before and after cataract surgery. Perceptual and Motor Skills 49, 699-704.

Arden G.B. (1979) Measuring contrast sensitivity with gratings: A new simple technique for the early diagnosis of retinal and neurological disease. J. Am. Optom. Assoc. 50, 35-39.

Arden G.B. and Lewis D.R.H. (1973) The pattern visual evoked response in the assessment of visual acuity. Trans. Ophthal. Soc. U.K. 93, 39-48.

Arend Jr. L.E. and Lange R.V. (1979) Phase-dependent interaction of widely separated spatial frequencies in pattern discrimination. Vision Res. 19, 1089-1092.

Arend Jr. L.E. and Lange R.V. (1980) Narrow band spatial mechanisms in apparent contrast matching. Vision Res. 20, 143-148.

Armington J.C. (1977) Visual cortical potentials and electroretinograms triggered by saccadic eye movements. In Visual Evoked Potentials in Man: New Developments (Edited by J.E. Desmedt). Pp. 286-300. Clarendon Press, New York.

Armington J.C., Corwin T.R. and Marsetta R. (1971) Simultaneously recorded retinal and cortical responses to patterned stimuli. J. Opt. Soc. Am. 61, 1514-1521.

Armington J.C., Gaarder K.K. and Schick A. (1967) Variation of spontaneous ocular and occipital responses with stimulus patterns. J. Opt. Soc. Am. 57, 1534-1539.

Arseni C., Crighel E., Matei M. and Dinu M. (1979) Influence of temporal lobe lesions on photic-evoked responses in occipital visual areas. Appl. Neurophysiol. 42, 145-152.

Ashworth B., Maloney A.F.J. and Townsend H.R.A. (1978) Delayed visual evoked potentials with bilateral disease of the posterior visual pathway. J. Neurol. Neurosurg. Psychol. 41, 449-451.

Atkinson J. and Campbell F.W. (1974) The effect of phase on the perception of compound gratings. Vision Res. 14, 158-162.

Bacon J.H. (1976) The interaction of dichoptically presented spatial gratings. Vision Res. 16, 337-344.

Barris M.C. and Dawson, W.W. (1980) Psychophysical and electrophysiological spatiotemporal response surfaces are identical. Invest. Ophthalmol. Visual Sci. (Suppl., April), 215.

Bauer Jr. J.A., Owens D.A., Thomas J. and Held R. (1979) Monkeys show an oblique effect. Perception 8, 247-253.

Bergen J.R., Wilson H.R. and Cowan J.D. (1979) Further evidence for four mechanisms mediating vision at threshold: Sensitivities to complex gratings and aperiodic stimuli. J. Opt. Soc. Am. 69, 1580-1587.

Berkeley M.A., Kitterle R. and Watkins D.W. (1975) Grating visibility as a function of orientation and retinal eccentricity. Vision Res. 15, 238-244.

Bisti S. and Maffei L. (1974) Behavioural contrast sensitivity of the cat in various visual meridians. J. Physiol. 241, 201-210.

Blake R. and Levinson E. (1977) Spatial properties of binocular neurons in the human visual system. Exp. Brain Res. 27, 221-232.

Blake R. and Rush C. (1980) Temporal properties of binocular mechanisms in the human visual system. Exp. Brain Res. 38, 333-349.

Blakemore C. and Hague B. (1972) Evidence for disparity detecting neurones in the human visual system. J. Physiol. 225, 437-455.

Bode H.W. (1945) Network Analysis and Feedback Amplifier Design. Pp. 220-221 and 403-450. D. Van Nostrand Company, New York.

Bodis-Wollner I. and Diamond S.P. (1976) The measurement of spatial contrast sensitivity in cases of blurred vision associated with cerebral lesions. Brain 99, 695-710.

Bodis-Wollner I., Hendley C.D. and Kulikowski J.J. (1972) Electrophysiological and psychophysical responses to modulation of contrast of a grating pattern. Perception 1, 341-349.

Boltz R.L., Harwerth R.S. and Smith III E.L. (1979) Orientation anisotropy of visual stimuli in rhesus monkey: A behavioral study. Science 205, 511-513.

Bostrom C., Keller E.L. and Marg E. (1978) A reconsideration of visual evoked potentials for fast automated ophthalmic refractions. Invest. Ophthalmol. Visual Sci. 17, 183-185.

Braccini C., Gambardella G. and Suetta G. (1980) A noise masking experiment in grating perception at threshold: The implications on binocular summation. Vision Res. 20, 373-376.

Braddick O., Campbell F.W. and Atkinson J. (1978) Channels in vision: basic aspects. In Handbook of Sensory Physiology (Edited by R. Held, H.W. Leibowitz and H.-L. Teuber). Vol. 8, pp. 1-38. Springer-Verlag, Berlin.

Breitmeyer B.G. and Ganz L. (1976) Implications of sustained and transient channels for theories of visual pattern masking, saccadic suppression, and information processing. Psychological Review 83, 1-36.

Burr D.C. (1980) Sensitivity to spatial phase. Vision Res. 20, 391-396.

Burton G.J. (1973) Evidence for non-linear response processes in the human visual system from measurements of spatial beat frequencies. Vision Res. 13, 1211-1226.

Burton G.J. (1976) Visual detection of patterns periodic in two dimensions. Vision Res. 16, 991-998.

Camisa J.M., Blake R. and Lema S. (1977) The effects of temporal modulation on the oblique effect in humans. Perception 6, 165-171.

Campbell F.W. and Maffei L. (1970) Electrophysiological evidence for the existence of orientation and size detectors in the human visual system. J. Physiol. 207, 635-652.

Campbell F.W. and Robson J.G. (1968) Application of fourier analysis to the visibility of gratings. J. Physiol. 197, 551-566.

Carlson C.R., Cohen R.W. and Gorog I. (1977) Visual processing of simple two-dimensional sine-wave luminance gratings. Vision Res. 17, 351-358.

Cavanagh P. (1978) Subharmonics in adaptation to sine wave gratings. Vision Res. 18, 741-742.

Ciganek L. (1971) Binocular addition of the visual response evoked by dichoptic patterned stimuli. Vision Res. 11, 1289-1298.

Cobb W.A., Morton H.B. and Ettlinger G. (1967) Cerebral potentials evoked by pattern reversal and their suppression in visual rivalry. Nature 216, 1123-1125.

Cormack R.H. and Blake R. (1980) Do the two eyes constitute separate visual channels? Science 207, 1100-1101.

Crawford M.L.J. and Cool S.J. (1970) Binocular stimulation and response variability of striate cortex units in the cat. Vision Res. 10, 1145-1153.

Creutzfeldt O.D. and Kuhnt U. (1973) Electrophysiology and topographical distribution of visual evoked potentials in animals. In Handbook of Sensory Physiology (Edited by R. Jung). Vol. VII/3, pp. 595-646. Springer-Verlag, New York.

Creutzfeldt O.D., Rosina S., Ito M. and and Probst W. (1969) Visual evoked response of single cells and of the EEG in primary visual area of the cat. J. Neurophysiol. 32, 127-139.

DeToledo-Morrell L., Hoeppner T.J. and Morrell F. (1979) Conditioned inhibition: Selective response of single units. Science 204, 528-530.

DeValois K.K., DeValois R.L. and Yund E.W. (1979) Responses of striate cortex cells to grating and checkerboard patterns. J. Physiol. 291, 483-505.

Diamond L. (1977) Latency of the steady state visual evoked potential. EEG Clin. Neurophysiol 42, 125-127.

Dobson J.S. and Davison P.A. (1980) A new rapid test of contrast sensitivity function utilizing spatial bandwidth equalization. Invest. Ophthalmol. Visual Sci. 19, 213-217.

Dowling J.E. (1970) Organization of vertebrate retinas. Invest. Ophthalmol. 9, 655-680.

Enoch J., Bedell H. and Kaufman H. (1979) Interferometric visual acuity testing in anterior segment disease. Arch. Ophthalmol. 97, 1916-1920.

Enoch J.M., Campos E.C., Greer M. and Trobe J. (1979) Measurement of visual resolution at high luminance levels in patients with possible demyelinating disease. Int. Ophthalmol. 1, 99-104.

Enoch J.M., Ohzu H. and Itoi M. (1979) Contrast (modulation) sensitivity functions measured in patients with high refractive error with emphasis on aphakia: I. Theoretical considerations. Doc. Ophthalmol. 47, 139-145.

Enoch J.M., Yamade S. and Namba A. (1979) Contrast (modulation) sensitivity functions measured in patients with high refractive error with emphasis on aphakia: II. Determinations on patients. Doc. Ophthalmol. 47, 147-162.

Facciolla D., Marciano F., Nolfe G. and Serra C. (1979) Visual evoked potentials in recent head injuries. Acta Neural. (Napoli) 34, 112-122.

Finette S., Harth E. and Csermely T.J. (1978) Anisotropic connectivity and cooperative phenomena as a basis for orientation sensitivity in the visual cortex. Biol. Cybernetics 30, 231-240.

Fiorentini A., Maffei L., Pirchio M. and Spinelli D. (1978) An electrophysiological correlate of perceptual suppression in anisometropia. Vision Res. 18, 1617-1621.

Fischer B. and Kruger J. (1979) Disparity tuning and binocularity of single neurons of cat visual cortex. Exp. Brain Res. 35, 1-8.

Frank Y. and Torres F. (1979) Visual evoked potentials in the evaluation of "cortical blindness" in children. Annals of Neurology 6, 126-129.

Franzen O. and Berkeley M. (1975) Apparent contrast as a function of modulation depth and spatial frequency: A comparison between perceptual and electrophysiological measures. Vision Res. 15, 655-660.

Frome F.W., Levinson J.Z., Danielson J.T. and Clavadetscher J.E. (1979) Shifts in perception of size after adaptation to gratings. Science 206, 1327-1329.

Gaskill J.D. (1978) Linear Systems, Fourier Transforms, and Optics. Pp. 107-134. J. Wiley and Sons, New York.

Ginsburg A.P., Cannon M.W. and Nelson M.A. (1980) Suprathreshold processing of complex visual stimuli: Evidence for linearity in contrast perception. Science 208, 619-621.

Glezer V.D. (1975) Reply to Tyler: Spatial frequency filters in cat visual cortex? Vision Res. 15, 305-307.

Glezer V.D. (1979) Selectivity for spatial frequency and bar width in cat visual cortex: Reply to Tyler. Vision Res. 19, 349-350.

Glezer V.D., Cooperman A.M., Ivanoff V.A. and Tscherback T.A. (1976) An investigation of spatial frequency characteristics of the complex receptive fields in the visual cortex of the cat. Vision Res. 16, 789-798.

Glezer V.D., Ivanoff V.A. and Tscherbach T.A. (1973) Investigation of complex and hypercomplex receptive fields of visual cortex of the cat as spatial frequency filters. Vision Res. 13, 1875-1904.

Gouras P. and Padmos P. (1974) Identification of cone mechanisms in graded responses of foveal striate cortex. J. Physiol. 238, 569-581.

Graham N. (1979) Does the brain perform a Fourier analysis of the visual scene? TINS, August, 207-208.

Graham N. and Nachmias J. (1971) Detection of grating patterns containing two spatial frequencies: A comparison of single-channel and multiple-channel models. Vision Res. 11, 251-259.

Graham N. and Rogowitz B.E. (1976) Spatial pooling properties deduced from the detectability of FM and quasi-AM gratings: A reanalysis. Vision Res. 16, 1021-1026.

Harter M.R. (1977) Binocular interaction: Evoked potentials to dichoptic stimulation. In Visual Evoked Potentials in Man: New Developments (Edited by J.E. Desmedt). Pp. 208-233. Claredon Press, Oxford.

Harter M.R., Conder E.S. and Towle V.L. (1980) Orientation-specific and luminance effects: Interocular suppression of visual evoked potentials in man. Psychophysiology 17, 141-145.

Harter M.R., Seiple W.H. and Musso M. (1974) Binocular summation and suppression: Visually evoked cortical responses to dichoptically presented patterns of different spatial frequencies. Vision Res. 14, 1169-1180.

Harter M.R., Seiple W.H. and Salmon L. (1973) Binocular summation of visually evoked responses to pattern stimuli in humans. Vision Res. 13, 1433-1446.

Henning G.B., Hertz B.G. and Broadbent D.E. (1975) Some experiments bearing on the hypothesis that the visual system analyses spatial patterns in independent bands of spatial frequency. Vision Res. 15, 887-897.

Hess R.F., Howell E.F. and Kitchin J.E. (1978) On the relationship between pattern and movement perception in strabismic amblyopia. Vision Res. 18, 375-377.

Hoekstra J., van der Goot D.P.J., van den Brink G. and Bilsen F.A. (1974) The influence of the number of cycles upon the visual contrast threshold for spatial sine wave patterns. Vision Res. 14, 365-358.

Hofmann H., Bartl G. and Gruber H. (1978) Objektive refraktometrie durch fernsehmuster-evozierte kortikale potentiale (Muster-VECP). Klin. Mbl. Augenheilk 172, 275-277.

Howell E.R. and Hess R.F. (1978) The functional area for summation to threshold for sinusoidal gratings. Vision Res. 18, 369-374.

Hubel D.H. and Wiesel T.N. (1977) Ferrier lecture: function architecture of macaque monkey visual cortex. Proc. R. Soc. Lond. B 198, 1-59.

Ikeda H., Tremain K.E. and Sanders M.D. (1978) Neuro-physiological investigation in optic nerve disease: Combined assessment of the visual evoked response and electroretinogram. Br. J. Ophthalmol. 62, 227-239.

Ingling Jr. C.R. (1978) Luminance and Opponent color contributions to visual detection and to temporal and spatial integration: Comment. J. Opt. Soc. Am. 68, 1143-1147.

Isono H. (1979) A re-examination of contrast threshold difference between spatial sine wave and square wave gratings. Vision Res. 19, 603-608.

Jones R. and Keck M.J. (1978) Visual evoked response as a function of grating spatial frequency. Invest. Ophthalmol. Visual Sci. 17, 652-659.

Julesz B. (1978) Global stereopsis: Cooperative phenomena in stereooptic depth perception. In Handbook of Sensory Physiology (Edited by R. Held, H.W. Leibowitz and H.-L. Teuber). Vol. 8, pp. 215-264. Springer-Verlag, Berlin.

Julesz B. and Caelli T. (1979) On the limits of Fourier decompositions in visual texture perception. Perception 8, 69-73.

Julesz B., Kropfl W. and Petrig B. (1980) Large evoked potentials to dynamic random-dot correlograms and stereograms permit quick determination of stereopsis. P.N.A.S. 77, 2348-2351.

Kadobayashi I., Mori M., Arima S. and Kato N. (1978) Visual evoked potential characteristics and subtypes of schizophrenia. Journal of Nervous and Mental Disease 166, 775-780.

Kataoka N., Yamauchi T., Takasaka Y., Kudoh T. and Harabayashi Y. (1979) Somatosensory and visual evoked potentials in temporal lobe epilepsy. Folia Psychiatrica et Neurologica Japonica 33, 251-254.

Kelly D.H. (1972) Adaptation effects on spatio-temporal sine-wave thresholds. Vision Res. 12, 89-101.

Kelly D.H. (1975) Spatial frequency selectivity in the retina. Vision Res. 15, 665-672.

Kelly D.H. (1976) Pattern detection and the two-dimensional Fourier transform: Flickering checkerboards and chromatic mechanisms. Vision Res. 16, 227-287.

Kelly D.H. (1977) Visual contrast sensitivity. Optica Acta 24, 107-129.

Kelly D.H. (1979a) Motion and vision. I. Stabilized images of stationary gratings. J. Opt. Soc. Am. 69, 1266-1274.

Kelly D.H. (1979b) Motion.and vision. II. Stabilized spatio-temporal threshold surface. J. Opt. Soc. Am. 69, 1340-1349.

Kelly D.H. and Magnuski H.S. (1975) Pattern detection and the two-dimensional Fourier transform: Circular targets. Vision Res. 15, 911-915.

King-Smith P.E. and Carden D. (1978) Luminance and opponent color contributions to visual detection and to temporal and spatial integration: Author's reply to comments. J. Opt. Soc. Am. 68, 1146-1147.

King-Smith P.E. and Kulikowski J.J. (1980) Pattern and movement detection in a patient lacking sustained vision. J. Physiol. 300, P60.

Kinney J.A.S. (1977) Transient visually evoked potentials. J. Opt. Soc. Am. 67, 1465-1474.

Klassen A., Heaney L.M., Lee M.C. and Torres F. (1979) Hypercapnic alteration of visual evoked responses in acute cerebral infraction. Arch. Neurol. 36, 627-629.

Klein S. and Stromeyer III C.F. (1980) On inhibition between spatial frequency channels: Adaptation to complex gratings. Vision Res. 20, 459-466.

Klingaman R.L. and Moskowitz-Cook A. (1979) Assessment of the visual acuity of human color mechanisms with the visually evoked cortical potential. Invest. Ophthalmol. Visual Sci. 18, 1273-1277.

Koenderink J.J., Bouman M.A., Dueno de Mesquita A.E. and Slappendel S. (1978) Perimetry of contrast detection thresholds of moving spatial sine wave patterns. J. Opt. Soc. Am. 68, 845-865.

Koenderink J.J. and van Doorn A.J. (1979) Spatiotemporal contrast detection threshold surface is bimodal. Optics Letters 4, 32-34.

Kojima M. and Zrenner E. (1980) Determinations of local thresholds in the visual field by recording the scotopic visually evoked cortical potential in man. Ophthalmic Res. 12, 1-8.

Kulikowski J.J. (1979) Spatial arrangement and spatial-frequency tuning of the cells in the cat visual cortex. Neuroscience Letters, Suppl. 3, S355.

Kulikowski J.J., Abadi R. and King-Smith P.E. (1973) Orientation selectivity of grating and line detectors in human vision. Vision Res. 13, 1478-1486.

Kulikowski J.J. and Bishop P.O. (1980) Interrelation between responses of simple cells in the cat visual cortex to bars, edges and gratings. Invest. Ophthalmol. Visual Sci. (Suppl., April), 223.

Kulikowski J.J. and King-Smith P.E. (1973) Spatial arrangement of line, edge and grating detectors revealed by subthreshold summation. Vision Res. 13, 1453-1478.

Lee S.I., Messenheimer J.A., Wilkinson E.C., Brickley Jr. J.J. and Johnson R.N. (1980) Visual evoked potentials to stimulus trains: Normative data and application to photosensitive seizures. EEG Clin. Neurophysiol. 48, 387-394.

Legatt A.D., Arezzo J. and Vaughan Jr. H.G. (1980) Averaged multiple unit activity as an estimate of phasic changes in local neuronal activity: Effects of volume-conducted potentials. J. Neuroscience Methods 2, 203-217.

Legge G.E. (1976) Adaptation to a spatial impulse: Implications for Fourier transform models of visual processing. Vision Res. 16, 1407-1418.

Legge G.E. (1978a) Sustained and transient mechanisms in human vision: Temporal and spatial properties. Vision Res. 18, 69-81.

Legge G.E. (1978b) Space domain properties of a spatial frequency channel in human vision. Vision Res. 18, 959-969.

Legge G.E. (1979) Spatial frequency masking in human vision: Binocular interactions. J. Opt. Soc. Am. 69, 838-847.

Lennerstrand G. (1978a) Binocular interaction studied with visual evoked responses (VER) in humans with normal or impaired binocular vision. Acta Ophthalmologica 56, 628-647.

Lennerstrand G. (1978b) Some observations on visual evoked responses (VER) to dichoptic stimulation. Acta Ophthalmol. 56, 638-647.

Lennie P. (1980) Parallel visual pathways: A review. Vision Res. 20, 561-594.

Lesevre N. and Joseph J.P. (1979) Modifications of the pattern-evoked potential (PEP) in relation to the stimulated part of the visual field (clues for the most probable origin of each component). EEG Clin. Neurophysiol. 47, 183-203.

Levi D.M., Harwerth R.S. and Smith E.L. (1979) Humans deprived of normal binocular vision have binocular interactions tuned to size and orientation. Science 206, 852-854.

Levinson J.Z. and Frome F.S. (1979) Perception of size of one object among many. Science 206, 1425-1426.

MacKay D.M. and Jeffreys D.A. (1973) Visually evoked potentials and visual perception in man. In Handbook of Sensory Physiology (Edited by R. Jung). Vol. VII/3, pp. 647-678. Springer-Verlag, New York.

Maffei L. (1978) Spatial frequency channels: Neural mechanisms. In Handbook of Sensory Physiology (Edited by R. Held, H.W. Leibowitz and H.-L. Teuber). Vol. 8, pp. 39-66. Springer-Verlag, Berlin.

Maffei L. and Campbell F.W. (1970) Neurophysiological localization of the vertical and horizontal visual coordinates in man. Science 167, 386-387.

Maffei L. and Fiorentini A. (1973) The visual cortex as a spatial frequency analyzer. Vision Res. 13, 1255-1268.

Maffei L., Morrone C., Pirchio M and Sandini G. (1979a) A perceptual phenomenon and its neurophysiological correlate. Perception 8, 43-46.

Maffei L., Morrone C., Pirchio M. and Sandini G. (1979b) Responses of visual cortical cells to periodic and non-periodic stimuli. J. Physiol. 283, 79-99.

Makous W. and Sanders R.K. (1978) Suppressive interactions between fused patterns. In Visual Psychophysics and Physiology (Edited by J.C. Armington, J. Krauskopfa and B.R. Wooten). Pp. 167-179. Academic Press, New York.

Martin J.I. (1970) Effects of binocular fusion and binocular rivalry on cortically evoked potentials. EEG Clin. Neurophysiol 28, 190-201.

May J.G., Cullen Jr. J.K., Moskowitz-Cook A. and Siegfried J.B. (1979) Effects of meridional variation on steady-state visual evoked potentials. Vision Res. 19, 1395-1402.

McCann J.J., Savoy R.L. and Hall Jr. J.A. (1978) Visibility of low-frequency sine-wave targets: Dependence on number of cycles and surround parameters. Vision Res. 18, 891-984.

Mecacci L. and Spinelli D. (1976) The effects of spatial frequency adaptation of human evoked potentials. Vision Res. 16, 477-479.

Meienberg O., Kutak L., Smolenski C. and Ludin H.P. (1979) Pattern reversal evoked cortical responses in normals: A study of different methods of stimulation and potential reproducibility. J. Neurol. 222, 81-93.

Mostafavi H. and Sakrison D.J. (1976) Structure and properties of a single channel in the human visual system. Vision Res. 16, 957-968.

Movshon J.A. and Lennie P. (1979) Pattern-selective adaptation in visual cortical neurones. Nature 278, 850-852.

Movshon J.A., Thompson I.D. and Tolhurst D.J. (1978a) Spatial summation in the receptive fields of simple cells in the cat's striate cortex. J. Physiol. 283, 53-77.

Movshon J.A., Thompson I.D. and Tolhurst D.J. (1978b) Receptive field organization of complex cells in the cat's striate cortex. J. Physiol. 283, 79-99.

Movshon J.A., Thompson I.D. and Tolhurst D.J. (1978c) Spatial and temporal contrast sensitivity of neurones in areas 17 and 18 of the cat's visual cortex. J. Physiol. 283, 101-120.

Nachmias J., Sansburg R., Vassilev A. and Weber A. (1973) Adaptation to square-wave gratings: In search of the elusive third harmonic. Vision Res. 13, 1335-1342.

Nachmias J. and Weber A. (1975) Discrimination of simple and complex gratings. Vision Res. 15, 217-224.

Naparstek Y., Shouval D., Auerbach E. and Eliakim M. (1979) Transient cortical blindness in hepatic encephalopathy. Israel J. Med. Sci. 10, 854-856.

Noda H., Creutzfeld O.D. and Freeman Jr. R.B. (1971) Binocular interaction in the visual cortex of awake cats. Exp. Brain Res. 12, 406-421.

Noda H., Freeman Jr. R.B., Gies B. and Creutzfeldt O.D. (1971) Neuronal responses in the visual cortex of awake cats to stationary and moving targets. Exp. Brain Res. 12, 389-405.

Noebels J.L., Roth W.T. and Kopell B.S. (1978) Cortical slow potentials and the occipital EEG in congenital blindness. Journal of the Neurological Sciences 37, 51-58.

Ochs A.L. (1979) Is Fourier analysis performed by the visual system or by the visual investigator? J. Opt. Soc. Am. 69, 95-98.

Ochs A.L. and Aminoff M.J. (1980) The effect of adaptation to the stimulating pattern of the latency and waveform of visual evoked potentials. EEG Clin. Neurophysiol. 48, 502-568.

Pantle A. (1973) Visual effects of sinusoidal components of complex gratings: Independent or additive? Vision Res. 13, 2195-2204.

Payne B.R., Elberger A.J., Berman N. and Murphy E.H. (1980) Binocularity in the cat visual cortex is reduced by sectioning the corpus callosum. Science 207, 1097-1099.

Poggio G.F. (1979) Mechanisms of stereopsis in monkey visual cortex. TINS, August, 199-201.

Quick R.F. and Reichert T.A. (1975) Spatial-frequency selectivity in contrast detection. Vision Res. 15, 637-643.

Ramirez R.W. (1974) The fast Fourier transform's error are predictable, therefore manageable. Electronics June 13, 96-102.

Regan D. (1977) Steady-state evoked potentials. J. Opt. Soc. Am. 67, 1475-1489.

Regan D. (1978) Assessment of visual acuity by evoked potential recording: Ambiguity caused by temporal dependence of spatial frequency selectivity. Vision Res. 18, 439-443.

Regan D., Whitlock J.A., Murray T.J. and Beverley K.I. (1980) Orientation-specific losses of contrast sensitivity in multiple sclerosis. Invest. Ophthalmol. Visual Sci. 19, 324-328.

Riggs L.A. (1974) Responses of the visual system to fluctuating patterns. Am. J. Opt. Physiol. Optics 5, 725-735.

Riggs L.A. (1977) Electrophysiological techniques for studying visual function in man: A historical overview. J. Opt. Soc. Am. 67, 1451-1457.

Riggs L.A. and Wooten B.R. (1972) Electrical measures and psychophysical data on human vision. In Handbook of Sensory Physiology (Edited by D. Jameson and L.M. Hurvich). Vol. VII/4, pp. 690-731. Springer-Verlag, New York.

Ross J. and Johnstone J.R. (1980) Phase and detection of compound gratings. Vision Res. 20, 189-192.

Rover J., Ostertag C., Schaubele G. and Klar M. (1978) Visuell evozierte potentiale beim kaninchen nac schadelhirntrauma. Bericht uber die Zusammenkunft der Deutschen Ophthalmologischen Gesellschaft 78, 528-531.

Samoilovich L.A. and Trush V.D. (1979) Cortical evoked potentials during consecutive visual masking. Fiziologiya Cheloveka 4, 267-274.

Sekuler R., Pantle A. and Levinson E. (1978) Physiological basis of motion perception. In Handbook of Sensory Physiology (Edited by H. Autrum, R. Jung, W.R. Lowenstein, D.M. MacKay and H.-L. Teuber). Vol. 8, pp. 67-96. Springer-Verlag, Berlin.

Seppalainen A.M., Raitta C. and Huuskonen M.S. (1979) n-Hexane-induced changes in visual evoked potentials and electroretinograms of industrial workers. EEG Clin. Neurophysiol. 47, 492-498.

Shagass C., Roemer R.A., Straumanis J.J. and Amadeo M. (1979) Temporal variability of somatosensory, visual, and auditory evoked potentials in schizophrenia. Arch. Gen. Psychiatry 36, 1341-1351.

Sherman J. (1979) Visual evoked potential (VEP): Basic concepts and clinical applications. J. Am. Opt. Assoc. 50, 19-118.

Shul'gina G.I. (1979) Slow potentials and spike activity of cortical neurons during development of internal inhibition. Zhurnal Vysshei Nervnoi Deyatel'nosti 26, 962-970.

Snyder A.W. and Srinivasan M.V. (1979) Human psychophysics: Functional interpretation for contrast sensitivity versus spatial frequency curve. Biol. Cybernetics 32, 9-17.

Sokol S. (1972) An electrodiagnostic index of macular degeneration. Arch. Ophthal. 88, 619-624.

Sokol S. (1976) Visually evoked potentials: Theory, techniques and clinical applications. Surv. Ophthalmol. 21, 18-44.

Sokol S. and Nadler D. (1979) Simultaneous electro-retinograms and visually evoked potentials from adult amblyopes in response to a pattern stimulus. Invest. Ophthalmol. Visual Sci. 18, 848-855.

Spekreijse H., van der Tweel L.H. and Zuidema T. (1973) Contrast evoked responses in man. Vision Res. 13, 1577-1602.

Spitzberg R. and Richards W. (1975) Broad band spatial filters in the human visual system. Vision Res. 15, 837-841.

Srebro R. (1978) The visually evoked response: Binocular facilitation and failure when binocular vision is disturbed. Arch. Ophthalmol. 96, 839-844.

Stecher S., Sigel C. and Lange R.V. (1973) Spatial frequency channels in human vision and the threshold for adaptation. Vision Res. 13, 1691-1700.

Steinberg R.H. (1965) Alternations of averaged photic evoked potentials in cat visual cortex during repetitive stimulation. EEG Clin. Neurophysiol. 18, 378-391.

Stromeyer III C.F. and Klein S. (1974) Spatial frequency channels in human vision as asymmetric (edge) mechanisms. Vision Res. 14, 1409-1420.

Stromeyer III C.F. and Klein S. (1975) Evidence against narrow-band spatial frequency channels in human vision: The detectability of frequency modulated gratings. Vision Res. 15, 899-910.

Stromeyer III C.F., Lange A.F. and Ganz L. (1973) Spatial frequency phase effects in human vision. Vision Res. 13, 2345-2360.

Sturr J.F. and Teller D.Y. (1973) Sensitization by annular surrounds: Dichoptic properties. Vision Res. 13, 909-918.

Switkes E., Mayer M.J. and Sloan J.A. (1978) Spatial frequency analysis of the visual environment: Anisotropy and the carpentered environment hypothesis. Vision Res. 18, 1393-1399.

Tangney J., Weisstein N. and Berbaum K. (1979) Masking independent of both separation and spatial frequency. Vision Res. 19, 817-824.

Tolhurst D.J. and Barfield L.P. (1978) Interactions between spatial frequency channels. Vision Res. 18, 951-958.

Tolhurst D.J., Sharpe C.R. and Hart G. (1973) The analysis of the drift rate of moving sinusoidal gratings. Vision Res. 13, 2545-2556.

Tyler C.W. (1975) Spatial frequency filters in cat visual cortex. Vision Res. 15, 303-304.

Tyler C.W. (1978a) An additional dimension to grating perception. Perception 7, 707-715.

Tyler C.W. (1978b) Selectivity for spatial frequency and bar width in cat visual cortex. Vision Res. 18, 121-122.

Tyler C.W., Apkarian P. and Nakayama K. (1978) Multiple spatial-frequency tuning of electrical responses from human visual cortex. Exp. Brain Res. 33, 535-550.

Tyler C.W., Apkarian P., Levi D.M. and Nakayama K. (1979) Rapid assessment of visual function: An electronic sweep technique for the pattern visual evoked potential. Invest. Ophthalmol. Visual Sci. 18, 703-713.

Uren S.M., Stewart P. and Crosby P.A. (1979) Subject cooperation and the visual evoked response. Invest. Ophthalmol. Visual Sci. 18, 648-652.

van der Tweel L.H., Estevez O. and Cavonius C.R. (1979) Invariance of the contrast evoked potential with changes in retinal illuminance. Vision Res. 19, 1283-1288.

van der Tweel L.H. and Verduyn Lunell F.E. (1965) Human visual responses to sinusoidally modulated light. EEG Clin. Neurophysiol. 18, 587-598.

van Lith G.H.M., van Marle G.W. and van Dok-Mak G.T.M. (1978) Variation in latency times of visually evoked cortical potentials. Brit. J. Ophthalmol. 62, 220-222.

Vassilev A. and Strashimirov D. (1979) On the latency of human visually evoked response to sinusoidal gratings. Vision Res. 19, 843-846.

Verzeano M., Dill R.C., Vallecalle E., Groves P. and Thomas J. (1968) Evoked responses and neuronal activity in the lateral geniculate. Experientia 24, 696-698.

von Knorring L. (1978) Visual averaged evoked responses in patients with bipolar affective disorders. Neuropsychobiology 4, 314-320.

Walker P. and Powell D.J. (1979) The sensitivity of binocular rivalry to changes in the nondominant stimulus. Vision Res. 19, 247-249.

Wanger P. and Nilsson B.Y. (1978) Visual evoked responses to pattern-reversal stimulation in patients with amblyopia and/or defective binocular functions. Acta Ophthalmol. 56, 617-627.

Watanabe A., Mori T., Nagata S. and Hiwatashi K. (1968) Spatial sine-wave responses of the human visual system. Vision Res. 8, 1245-1263.

Watson A.B. and Nachmias J. (1980) Summation of asynchronous gratings. Vision Res. 20, 91-94.

Weisstein N., Harris C.S., Berbaum K., Tangney J. and Williams A. (1977) Contrast reduction by small localized stimuli: Extensive spatial spread of above-threshold orientation-selective masking. Vision Res. 17, 341-350.

Westheimer G. (1978) Spatial phase sensitivity for sinusoidal grating targets. Vision Res. 18, 1073-1074.

White K.D., Petry H.M., Riggs L.A. and Miller J. (1978) Binocular interactions during establishment of McCollough effects. Vision Res. 18, 1201-1215.

Wilson H.R. and Bergen J.R. (1979) A four mechanism model for threshold spatial vision. Vision Res. 19, 19-32.

Wolfe P. (1979) Utilizing the visual evoked response (VER) for visual fields when subjective responses are not attainable. J. Am. Optom. Assoc. 50, 117-118.

Wright J.J., Craggs M.D. and Sergejew A.A. (1979) Visual-evoked response in lateral hypothalamic neglect. Experimental Neurology 65, 178-185.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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